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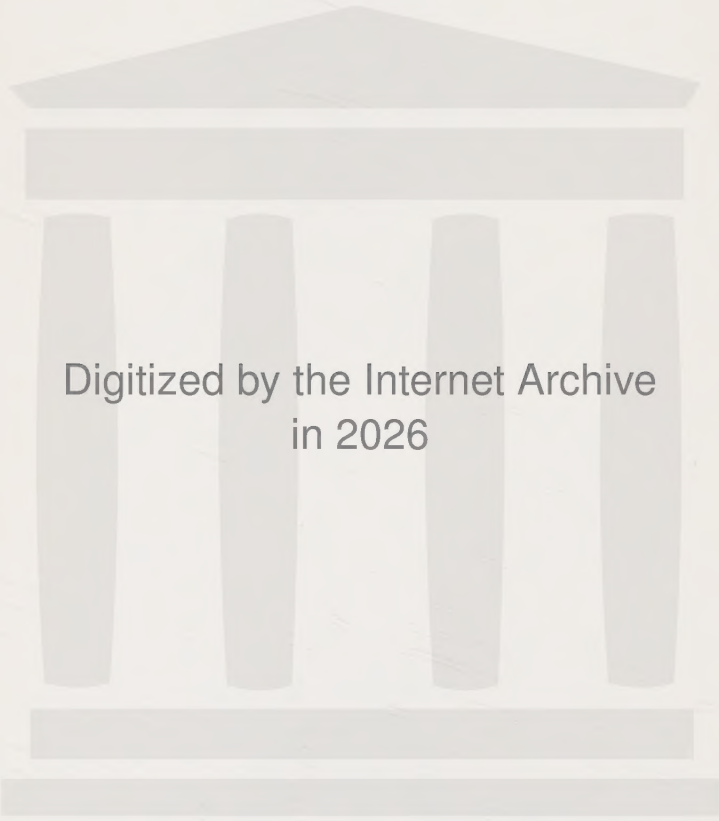
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QUANTITATIVE
AND
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ECOLOGY

QUANTITATIVE AND DYNAMIC ECOLOGY

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Preface

THE study of Ecology now necessitates a knowledge of many sciences in addition to Botany and Zoology and with the rapid development of statistics the student of Ecology is often faced with the problem of using and understanding the simpler statistical procedures which are in common use.

The aim of this book is to present the general theoretical concepts that have been formulated in relation to plant ecology together with the approaches and statistical methods that have been used in developing these concepts. The early work in plant ecology was, of necessity, largely concerned with the description of vegetation in relation to the environment. This branch of ecology is still very actively pursued and will continue to be of importance until all vegetation is described on a world-wide basis. From this early descriptive ecology came a realization of the difficulties of sampling vegetation and its dynamic nature, and consequently sampling methods were developed and tested and different measures of the abundance of a species devised. The concept of plant succession was also developed from this early descriptive work and pointed the way to many of the concepts in use today. With the basic idea of a dynamic vegetation accepted, further examination in still greater detail outlined some of the processes involved and demonstrated the close inter-relationships that exist between species and between individuals of the same species. On reaching this level of development the necessity for sensitive sampling measures and statistical procedures to extract from a mass of data the relevant information became of paramount importance.

This book follows the general sequence of development outlined above. The early chapters are concerned with the methods of describing vegetation and the problem of sampling. The subsequent chapters deal with the fundamental concepts in use today. These include succession, cyclic change, plant interactions and the non-random distribution of individuals of a species in vegetation. The final chapters outline the controversy over the validity of the plant community as a distinct and recognizable entity and the methods that have been employed in this branch of ecology.

No detailed description of vegetation types or account of environmental factors and their measurement is attempted—both these aspects of ecology are now so extensive as to merit a book to themselves.

Finally, it gives me considerable pleasure to thank Dr. N. Waloff of the

Department of Zoology, Imperial College, for her reading of the draft manuscript and her many valuable criticisms and suggestions. I also owe a considerable debt to Dr. A. J. Rutter of this Department for the many hours he has spent in criticizing and discussing various sections of this book.

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London, S.W.7
1964

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1 The Description of Vegetation

A CONSIDERABLE proportion of all ecological work in the past and to a considerable extent at the present time, has been directed towards the description of vegetation. The object of such description is to enable people other than the observer to build a mental picture of an area and its vegetation and to allow the comparison and ultimate classification of different units of vegetation. Before any serious or detailed work can be commenced in an area it is necessary to know what species are present, what is their distribution and what is the relative degree of abundance of each species. Additional information on the morphology of the species characteristic of the area and a general account of the environment is also essential. Thus the *Floristic* composition, simply expressed as a list of species, *Life form* composition and *Structure* of vegetation are a necessary basis of all ecological work; this approach to ecology has dominated the subject until quite recently and will continue to be prominent until an adequate description of all vegetation both on a regional and on a world-wide basis is completed.

LIFE FORM

The best-known description and classification of life forms, and the use of life form to construct a *biological spectrum* are due to Raunkiaer (1909, 1928, 1934). He arranged the life forms of species in a natural series in which the main criterion was the height of perennating buds, and he showed that this criterion appeared to reflect adaptation to climate. He based this series on the assumption that the original environment was considerably more moist and uniformly hot than it is now, and accordingly the most primitive life form is that which dominates tropical vegetation at the present time. Conversely the more highly evolved species are found in the colder areas of the world. Raunkiaer established the following types (see also Fig. 1.1):

1. *Phanerophytes*

The perennating buds or shoot apices borne on aerial shoots.

(a) EVERGREEN PHANEROPHYTES without bud scales (tropical tree species)

(b) EVERGREEN PHANEROPHYTES with bud scales

1—Q.D.E.

(c) DECIDUOUS PHANEROPHYTES with bud scales

(Each of the above groups can be sub-divided into Nanophanerophytes (< 2 m in height), Microphanerophytes (2–8 m), Mesophanerophytes (8–30 m) and Megaphanerophytes (> 30 m in height). Two further groups are usually included—epiphytic Phanerophytes and stem-succulent Phanerophytes.)



Fig. 1.1. The relative positions of the perennating parts of four life forms. (1) Phanerophytes, (2–3) Chamaephytes, (4) Hemicryptophytes and (5–9) Cryptophytes. The persistent axes and surviving buds are shown in black. (From Raunkiaer 1934; courtesy of Oxford Clarendon Press.)

2. *Chamaephytes*

Perennating buds or shoot apices borne very close to the ground.

(a) **SUFFRUTICOSE CHAMAEPHYTES.** Characterized by more or less erect aerial shoots which die away in part at the onset of an unfavourable season of the year. Perennating buds arise on the lower portions of the erect stems where they are less exposed to the environment. Very characteristic of many parts of the Mediterranean.

(b) **PASSIVE CHAMAEPHYTES.** Similar to the last group but at the onset of adverse conditions the weakened erect axes fall over and buds arise along the horizontal stems where at ground level they obtain some protection from the environment; e.g. *Stellaria holostea*.

(c) **ACTIVE CHAMAEPHYTES.** The vegetative shoots are persistently orientated along the ground usually rooting along their length; e.g. *Lysimachia nummularia*, *Empetrum nigrum*.

(d) **CUSHION PLANTS.** Basically a reduced and very compacted form of the last group.

3. *Hemicryptophytes*

Perennating buds at ground level, all above ground parts dying back at the onset of unfavourable conditions. Stolons may or may not be present.

(a) PROTO HEMICRYPTOPHYTES. Lowermost leaves on stem less perfectly developed than the upper ones, the perennating buds arise at ground level; e.g. *Rubus idaeus*.

(b) PARTIAL ROSETTE PLANTS. The best developed leaves form a rosette at the base of the aerial shoot, but some leaves are present on the aerial stems; e.g. *Ajuga reptans*, *Achillea millefolium*, etc.

(c) ROSETTE PLANTS. The leaves are restricted to a rosette at the base of the aerial shoot; e.g. *Bellis perennis*, *Taraxacum officinale*, *Hypochaeris radicata*, etc.

4. *Cryptophytes*

Perennating buds below ground level or submerged in water.

(a) GEOPHYTES. Rhizome, bulb or tuber geophytes, over-wintering by food stores under ground from which arise the buds to produce the next season's aerial shoots.

(b) HELOPHYTES. Those plants which have their perennating organs in soil or mud below water-level with aerial shoots above water-level; e.g. *Typha*, *Alisma*, etc.

(c) HYDROPHYTES. Those plants with their perennating buds under water, and with their leaves submerged or floating. The buds may occur on rhizomes as in *Nuphar*, *Nymphaea*, etc. or winter buds may become detached from the plant and sink to the bottom of the water and there survive the unfavourable season (*Potamogeton obtusifolius*, *P. pusillus*, etc.).

5. *Therophytes*

Annual species which complete a life history from seed to seed during the favourable season of the year. Their life span can be as short as a few weeks, and they are characteristic of desert regions and cultivated soil where the interference of man protects them from their (slower growing) natural competitors.

Using the life form as a basis of comparison it is possible to compare areas which are widely separated geographically and do not contain species common to both (the normal basis of comparison of areas). The life form is assumed to have evolved in direct response to the climatic environment and accordingly the proportion of life forms in an area will give a good indication of its climatic zone. Thus the biological spectrum is a useful measure for comparison on a geographical scale and shows the number of species within each life form group (Table 1.1).

Table 1.1—The percentage representation of different life forms in the flora of Denmark (1,084 species) and St. Thomas and St. Jan, West Indies (904 species). (From Raunkiaer 1934; courtesy of Oxford Clarendon Press)

	Denmark	St. Thomas and St. Jan
Mega and Mesophanerophytes (MM)	1	5
Microphanerophytes (M)	3	23
Nanophanerophytes (N)	3	30
Epiphytes (E)	0	1
Stem succulents (S)	0	2
Chamaephytes (Ch)	3	12
Hemicryptophytes (H)	50	9
Geophytes	11	3
Hydrophytes and Helophytes (HH)	11	1
Therophytes (Th)	18	14

Raunkiaer gives several interesting examples from which he concludes that the zonation of vegetation progresses from a Phanerophytic type in the tropical zone to Therophytic in the sub-tropical desert areas, Hemicryptophytic in the cold temperate and finally a Chamaephytic type in the cold zone (Table 1.2). Similar trends can be seen with increase in altitude which

Table 1.2—The biological spectrum for different geographical zones. (From Raunkiaer 1934; courtesy of Oxford Clarendon Press)

Area	Percentage distribution of the species among the life forms (Key to symbols in Table 1.1)										
	S	E	MM	M	N	Ch	H	G	HH	Th	
Seychelles	1	3	10	23	24	6	12	3	2	16	Tropical forest
St. Thomas and St. Jan.	2	1	5	23	30	12	9	3	1	14	Tropical forest
Ellesmereland	—	—	—	—	—	23.5	65.5	8	3	—	Tundra
Baffinland	—	—	—	—	1	30	51	13	3	2	Tundra
Death Valley, California	3	—	—	2	21	7	18	2	5	42	Desert
Libyan Desert				3	9	21	20	4	1	42	Desert

reflects the increasing severity of the climate. Thus there are more Chamaephytes and correspondingly fewer Hemicryptophytes, with increase in altitude in the alps (Table 1.3). In general the life form spectrum is not of great significance in comparing adjacent areas of vegetation but is of value in the realm of 'Plant Geography'.

Table 1.3—The biological spectrum at different altitudes in the Alps. (From Raunkiaer 1934; courtesy of Oxford Clarendon Press)

The nival region of the Alps	Percentage distribution of the species among the life forms (Key to symbols in Table 1.1)									
	S	E	MM	M	N	Ch	H	G	HH	Th
Above 3,600 m						67	33			
3,300–3,600 m						58	42			
3,150–3,300 m						58	42			
3,000–3,150 m						52.5	45			2.5
2,850–3,000 m						33	62	2		3
2,700–2,850 m						33	61	3		3
2,550–2,700 m					0.5	28	65.5	2		4
2,400–2,550 m					1	24	67	4	0.3	4

STRUCTURE

The structure of vegetation is defined by three components: the vertical arrangement of species, i.e. the stratification of the vegetation; the horizontal arrangement of species, i.e. the spatial distribution of individuals; and, finally, the abundance of each species. The latter component of vegetation can be expressed in several ways, ranging from a direct count of the number of individuals in an area (density) to the dry weight of vegetable material produced in a given area (yield).

STRATIFICATION OF VEGETATION

A casual inspection of a woodland will demonstrate the marked stratification of the vegetation ranging from two layers (a herb layer at ground level and the canopy of the tree layer) to a more complicated arrangement with a herb layer, several shrub and sapling layers, and the overall canopy of the tree layer. In tropical forest the stratification of the vegetation has been long recognized as one of its characteristic features, though the variation of height within any one stratum has led to some argument as to the distinctness of the various strata recognized by different workers. The same criteria of layering can be applied to herbaceous vegetation and detailed description of the stratification of vegetation forms an important part in the understanding and recording of its structure. The method of description of the stratification of forest vegetation is due to Davis and Richards (1933–4) who constructed to scale, profile diagrams taken from narrow sample strips of tropical forest. (The concept of stratification is of obvious importance in any consideration of tropical forest and accordingly most of the published work on this topic relates to this type of vegetation.) The method consists of laying out a narrow rectangular

sample plot, of required length and width (usually not less than 60 m in length, and 8 m has been found to be a convenient width). All vegetation lower than a chosen arbitrary height is cleared away, the remaining trees and shrubs being carefully mapped and the diameters of the trunks noted. The total height, height to first large branch, lower limit of crown and width of crown are measured. To obtain these measures it is often necessary to fell all the trees in the strip, commencing with the smallest trees so as to avoid the crushing of these smaller trees by the larger. From the measurements obtained an accurate scaled profile diagram can be obtained showing the spatial relation of the different species to each other both in a horizontal sense as well as a vertical sense.

Tropical forest is usually divided into five layers *A*, *B*, *C*, *D* and *E* (see Richards 1962). The *A* layer is composed of the tallest trees present in the area (usually termed 'emergents'), the *B* and *C* layers form two strata of tree species, *D* the shrub layer and *E*, the lowest stratum, the ground or field layer. Two examples of profile diagrams are given below (Figs. 1.2 and 1.3) taken from Richards (1936) and Beard (1949) and illustrate the



Fig. 1.2. Profile diagram of primary forest in Borneo representing a strip of forest 61 m long and 7.6 m wide. (From Richards, 1936; courtesy of *J. Ecol.*)

differences between primary mixed Dipterocarp forest in Borneo, having a distinct though discontinuous *A* layer with a continuous *B* and *C* layer and a single-dominant forest (*Dacryodes-Sloanea* association) in Dominica,



Fig. 1.3. Profile diagram of primary forest in the West Indies representing a strip of forest 7.6 m wide. (From Beard 1949; courtesy of *Oxf. For. Mem.*)

British West Indies, which has a well marked continuous *A* layer and clear *B* and *C* layers.

Profile diagrams can also be usefully employed in vegetation of lower stature to illustrate the relationship between topography and the distribution of individuals of a species, or the distribution of root systems in relation to the topography and drainage of an area. Thus, the distribution of vegetation in relation to hummocks in calcareous mire in Teesdale (Pigott 1956) is very conveniently expressed as a diagram (Fig. 1.4).

A simultaneous approach to stratification of vegetation, abundance and to spatial distribution of each species can be made in a way suggested by Christian and Perry (1953) who developed a method especially suitable for large-scale surveys. Letters and figures are assigned to the tree, the shrub and ground stories, to their component layers and to the density of each. Thus, A_1 is used for low trees, A_2 for medium sized trees and A_3 for tall trees. Similarly, B_1 , B_2 , B_3 and C_1 , C_2 , C_3 are used for low, mid-height and tall shrubs and herbs respectively. Heights can be recorded for each stratum as mean values. Thus, A_3^{15} would represent a tall tree 15 m in height, etc. Density is similarly treated by prefixing *x*, *y* or *z* for dense, average or sparse and *xx* or *zz* for very dense and very sparse respectively. Thus a complex community with two tree layers, three shrub layers and two grass layers at varying densities would be written as

$$A_3^{60}z, A_2^{30}y, B_3^8z, B_2^3x, B_1^1x, C_2^{1zz}, C_1^{3zz}.$$

This method has been used in a series of vegetational surveys in northern Australia and offers a good shorthand method of describing the physiognomy of the vegetation, the more abundant species of any layer being

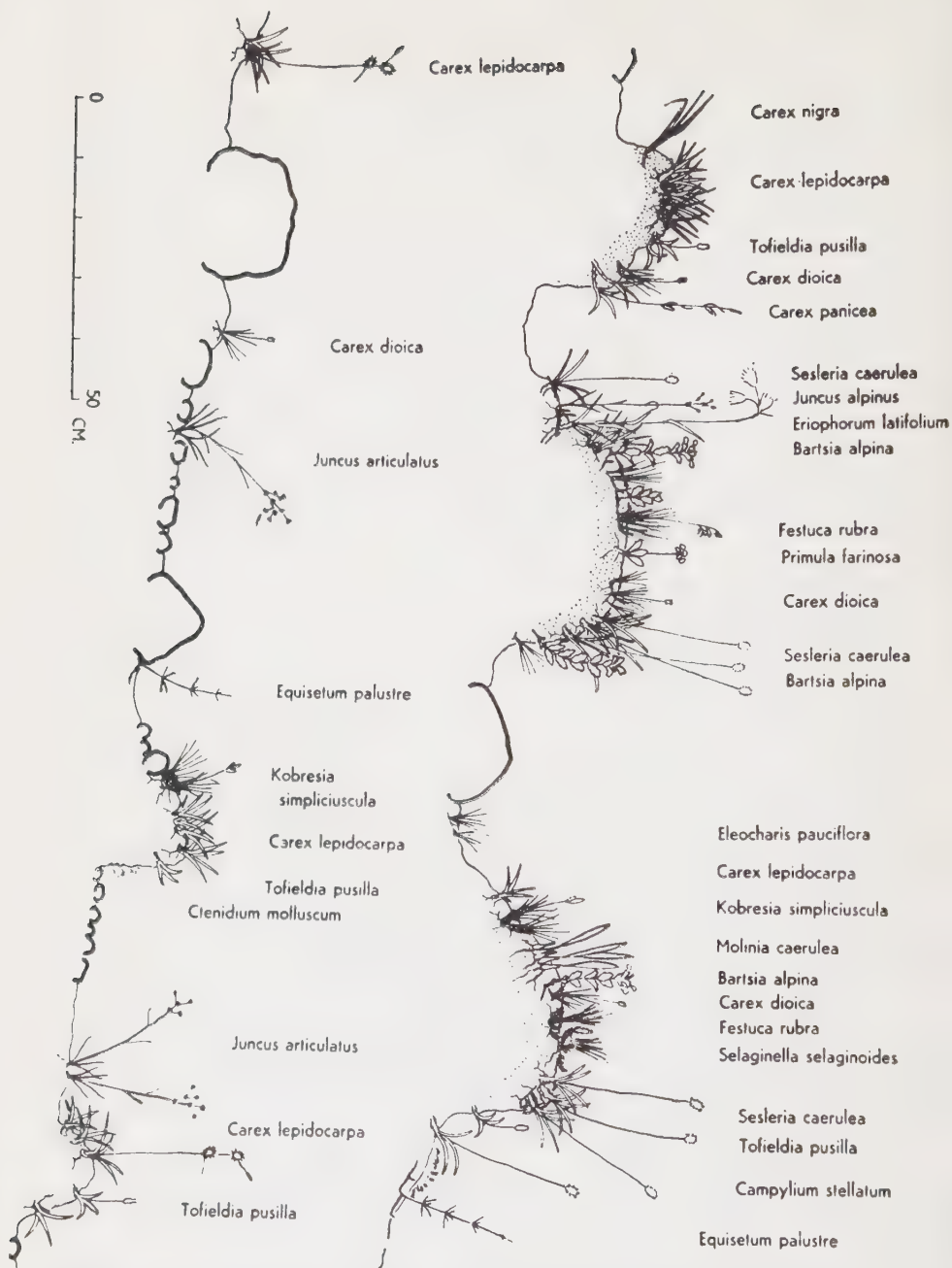


Fig. 1.4. Profile diagram through the hummock complex at the upper margin of a small calcareous marsh. The depth of the humus-stained part of the hummocks is indicated by stippling. The lower diagram is a direct continuation along the same line as the upper. (From Pigott 1956; courtesy of *J. Ecol.*)

appended to the formula. It is clear that the height groups are quite arbitrary and that the errors associated with such visual assessments should be controlled by collaboration between different field workers. Comparisons of descriptions of the same stand made by different workers would reduce the errors to a minimal level, and accordingly increase the value of the method.

HORIZONTAL DISTRIBUTION—MAPPING TECHNIQUES

The detailed mapping of vegetation is obviously a very laborious and time-consuming operation and its use is normally reserved for the detailed study of small areas of vegetation made over a period of years. The mapped areas are in the form of 'permanent quadrats'. Permanent quadrats are established and carefully marked out in such a manner as to enable the exact position to be located again in subsequent years. Each individual plant, or shoot, or clump of shoots is recorded accurately. This enables a composite picture of change in vegetation with time to be built up. It is advisable to sub-divide the permanent quadrat to facilitate the positioning of individuals within the area, and similarly it is more convenient to record the actual positions of the individual plants on 'ruled square' paper. The relationship between *Festuca ovina* and *Hieracium pilosella* in grassland after the removal of rabbit grazing has been investigated by Watt (1962) who gives a series of permanent quadrats recorded at intervals from 1946 onwards (Fig. 1.5). The permanent quadrats show quite clearly the change over the years of the relative abundance of the two species.

In general, the use of both permanent quadrats and the mapping of vegetation, as descriptive techniques should be limited to those problems where the vegetational change is likely to be fairly rapid and at the same time very marked. Where vegetational change is less marked more refined techniques are necessary (see p. 14).

THE SUBJECTIVE ASSESSMENT OF ABUNDANCE

Frequency symbols

The simplest and most rapid way of describing vegetation is to list the species present within a sample area and to attach to each species a subjective assessment of its abundance. This method of approach has been used by numerous workers and several convenient classes of plant abundance have been employed. One of the most widespread of the subjective ratings used by British ecologists employs five classes of abundance, Dominant, Abundant, Frequent, Occasional and Rare with prefixes 'very' and 'locally' to qualify distribution and abundance where necessary. Thus

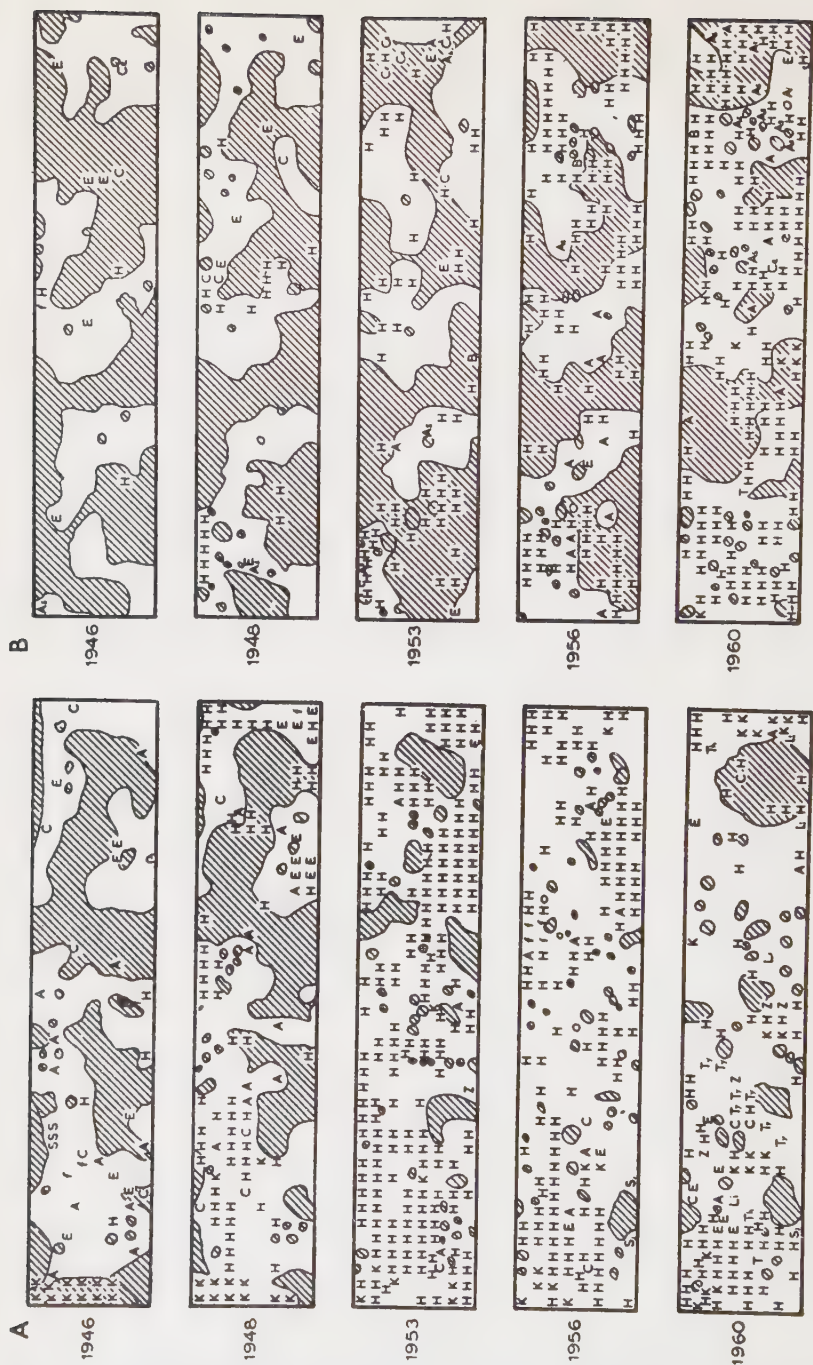


Fig. 1.5. The use of permanent quadrats to show the change of abundance of *Festuca* (shaded) and *Hieracium* (H) in enclosed (A) and control (B) plots. (From Watt 1962; courtesy of *J. Ecol.*)

a species of clumped habit, scattered over the area, would be referred to as locally frequent. Further classes can be used if thought necessary but it becomes increasingly difficult to distinguish between adjacent abundance classes as the total number of such classes increases. This in fact is one of the great weaknesses of this method of assessing the relative abundance of a species, and it is clear that other factors will often unknowingly influence the judgement of an observer. Small species tend to be rated lower than conspicuous ones, and similarly a species in full flower receives a higher rating than one which was in a vegetative state at the time of sampling.

Again, species that form obvious clumps are more conspicuous than species that are more evenly scattered and would be preferentially classed in an abundance scale. Thus such visual assessment of species abundance in an area includes a large unconscious error of judgement reflecting size, pattern of distribution and state of flowering of the species under consideration. Further the assessment is not constant from person to person, and a species that is referred to as 'Frequent' by one field worker may well be classed as 'Abundant' or 'Occasional' by others. This problem has been discussed by Hope-Simpson (1940) who investigated the causes of error in subjective assessment of abundance, including such effects as annual fluctuation, seasonal change and choice of sampling site. These latter errors are common to most measures of plant abundance and do not concern us here. However, comparisons of the data, derived from 'ordinary' and 'specially careful' recordings, illustrate the inconsistency of subjective methods. It is possible to compare the data if one establishes 'agreement classes' rated as 'Exact', 'Approximate', 'Intermediate' agreement or complete 'Disagreement'.

Table 1.4—Comparison by agreement classes expressed as a percentage of the total number of species
(From Hope-Simpson 1940; courtesy of *J. Ecol.*)

	Comparison of two independent samples from the same site	Comparison of ordinary and specially careful recording
Exact agreement	44	36
Approximate agreement	8	12
Intermediate	36	38
Disagreement	12	14

The data shows clearly that subjective assessment of plant abundance contains a very large error and will, at the most, only give an approximate indication of abundance. Accordingly the use of frequency symbols should be strictly limited to initial description, and the degree of error present

always borne in mind. A further drawback to the method lies in the rather unfortunate choice of the word 'Dominant' as the class representing the most abundant species, since in addition to the meaning here (the most abundant in a physiognomic sense) it is often confused with dominant in a sociological sense, meaning that species which exerts the most influence on the other species of the community. A species may be dominant in both senses of the word, but this need not necessarily be the case. For example Pearson (1942) has shown that regeneration of *Pinus ponderosa* depends on the type of ground vegetation. No regeneration occurs where the ground vegetation is *Festuca arizonica*, a species which grows during both the dry and the wet season, and can successfully compete with pine seedlings and prevent their establishment. On the other hand there is active regeneration when the ground vegetation is *Muhlenbergia montana* which only grows during the 'wet' season when water is plentiful for both species. In a sociological sense the dominant species is *Festuca arizonica*, whereas the immediate visual impression would put *Pinus* as the dominant. In many instances it is legitimate to equate the two definitions of 'dominant' but this is by no means always justified as the above example demonstrates. A further confusion that may arise is by the use of the word dominant in forestry literature as applied to a forest canopy, where those trees whose crowns are more than half exposed to full illumination are often referred to as 'dominants' (see Richards *et al.* 1940). It is usual that a dominant species of tree in the latter sense is one which is dominant in a sociological sense (one exception is given above), and thus it is recommended that 'dominant' as a frequency symbol be rejected—it can be very readily replaced by the term 'very abundant', which to all intents and purposes is synonymous.

Braun-Blanquet's system of rating

A more elaborate and better defined approach has been suggested by Braun-Blanquet (1927) who proposed what is now a recognized procedure for describing a stand of vegetation (see also Poore 1955). Two scales are used, one combining the number and cover of a species, and the second giving a measure of the grouping:

- + = sparsely or very sparsely present; cover very small
- 1 = plentiful but of small cover value
- 2 = very numerous, or covering at least $\frac{1}{20}$ of the area
- 3 = any number of individuals covering $\frac{1}{4}$ to $\frac{1}{2}$ of the area
- 4 = any number of individuals covering $\frac{1}{2}$ to $\frac{3}{4}$ of the area
- 5 = covering more than $\frac{3}{4}$ of the area

Soc. 1 = growing singly, isolated individuals

Soc. 2 = grouped or tufted

Soc. 3 = in small patches or cushions

Soc. 4 = in small colonies, in extensive patches, or forming carpets

Soc. 5 = in pure populations

The assessment of plant abundance and distribution is obtained from a series of adjacent quadrats of increasing size which are laid down so as to continuously increase the sample area (Fig. 1.6). An exact list of all plant

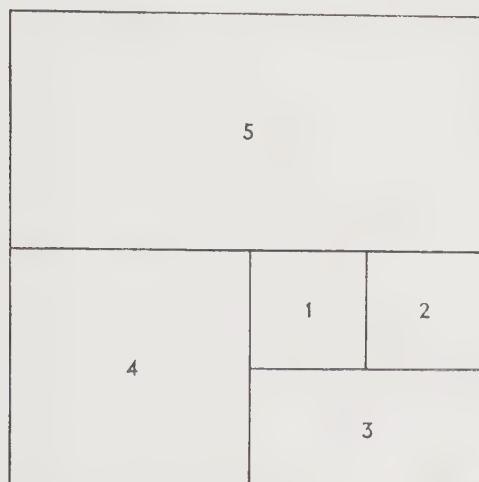


Fig. 1.6. The systematic arrangement of a series of quadrats to successively increase the size of the sample area. (From Poore 1955; courtesy of *J. Ecol.*)

species including lichens and bryophytes, with an attendant visual estimate of their sociability and abundance, is taken from the sample area. The measure of plant abundance used here is a definite improvement on the more traditional approach outlined previously. The scale combines, in part, abundance (number) with coverage of the area. It separates these to some extent from pattern of distribution and plant size which bias to an undefined extent the earlier abundance scale used. Accordingly the Braun-Blanquet scale has much to recommend it for a rapid survey of large areas of vegetation, since with practice it is possible for an individual recorder to minimize error from site to site. However, unconscious errors due to bias of different recorders will always be present and the extent to which they detract from the value of the method will remain debatable.

The Braun-Blanquet scale has several modifications and one of the more widely used scales, i.e. the Domin scale, is set out in Table 1.5.

The increased number of divisions enables a more detailed assessment to be made of plant coverage and field workers claim a high degree of accuracy can be obtained with sufficient experience. The Domin scale has

Table 1.5

	Domin scale	Braun-Blanquet
Cover about 100 per cent	10 }	5
Cover > 75 per cent	9 }	
Cover 50-75 per cent	8 }	4
Cover 33-50 per cent	7 }	
Cover 25-33 per cent	6 }	4
Abundant, cover about 20 per cent	5 }	
Abundant, cover about 5 per cent	4 }	2
Scattered, cover small	3 }	
Very scattered, cover small	2 }	1
Scarce, cover small	1 }	
Isolated, cover small	X	X

the additional advantage in that it can be directly converted into the Braun-Blanquet scale wherever necessary and enable direct comparison of different sets of data.

QUANTITATIVE ASSESSMENT OF ABUNDANCE

Since the realization that a large degree of error is inherent in subjective evaluation of abundance, ecologists have become increasingly conscious of the necessity of using quantitative measures to describe vegetation. The question as to which abundance measure should be used is often affected by the time it takes to obtain a sample of the population of adequate size, and it is true to say that the better quantitative measures available to ecologists are certainly but unavoidably time consuming.

Density

This is a count of the number of individuals within an area. It is usual to count the number of individuals within a series of randomly distributed quadrats, calculating the average number of individuals relative to the size of quadrat used, from the total sample. The method is accurate, allows direct comparison of different areas and different species and is an absolute measure of the abundance of a plant. The disadvantage of the method is usually associated with the time involved in counting what, potentially, can be very large numbers of individuals. This can in part be circumvented by counting within small quadrats, but there always remains those cases where the 'individual' cannot be picked out with any great degree of certainty, e.g. *Vaccinium myrtillus*, many grasses, sedges, etc. In some instances a convenient unit of the vegetation can be used instead of the complete individual; thus, individual tillers, flowering culms, erect shoots, or, indeed, whole clumps could be a suitable reflection of the density of a species. When these approaches fail, as for example with a species such as *Festuca rubra*, it is necessary to find an alternative approach.

Cover

This is defined as the proportion of the ground occupied by perpendicular projection on to it of the aerial parts of individuals of the species under consideration (Greig-Smith 1957). It is in fact an estimation of the area covered by given species, usually expressed as a percentage of the total area and estimated from a number of sample points. The cover value can be obtained either by a visual estimate, a certain percentage of the total area of a quadrat being covered by a given species, or measured by taking a number of points from the sample area and determining at those points which species if any is covering the surface of the ground. Visual estimates are obviously subject to the same personal bias as has been discussed already in relation to frequency symbols (p. 11) and should be avoided where possible, despite their relative speed and ease of use. Measures of cover are conveniently obtained using a frame of pins that can be adjusted to the height of the vegetation. The pins are lowered one at a time, and the species touched by each pin in turn recorded. The final number of 'hits' from a number of sample 'frames' is then expressed as a percentage of the total number of pins. It should be noted that the total percentage cover for all species in an area will nearly always exceed 100 per cent since in closed vegetation leaves of several different species frequently overlap one another at a particular point.

Table 1.6—The dependence of estimated cover on the diameter of pin
(From Goodall 1952, courtesy of *Austr. J. Sci. Res.*)

Locality	Species	Number of points	Estimated cover using pin different diameters (mm)		
			0	1.84	4.75
Seaford	<i>Ammophila arenaria</i>	200	39.0	66.5	71.0
	<i>Ammophila arenaria</i>	200	60.5	74.0	82.0
Black Rock	<i>Ehrharta erecta</i>	200	74.5	87.0	93.5
Sorrento	<i>Lepidosperma concavum</i>	200	19.5	22.0	27.5
	<i>Spinifex hirsutus</i>	200	35.0	48.5	61.0
Carlton	<i>Fumaria officinalis</i>	200	20.5	31.5	30.0
	<i>Ehrharta longiflora</i>	200	24.5	25.5	37.5
	No contact	200	53.0	42.5	38.5
	<i>Lolium perenne</i>	200	65.0	85.5	82.5

The main error involved in this measure of plant abundance (apart from small personal errors which are inevitably present and are only of any consequence in tall vegetation) is the exaggeration of the estimate of percentage cover when a large diameter pin is used (Goodall 1952*a*). Goodall gives the data on the effect of pin diameter in Table 1.6.

For the majority of the species there is a considerable difference which is statistically significant, between the percentage cover estimate obtained by using an optical cross-wire apparatus sighted on to the vegetation (0 mm pin diameter) and the percentage cover reading given by the pins. This is simply due to the area of the tip of the pin being finite instead of zero. If absolute measures of percentage cover are required it is important to use an optical method, which will give a reliable measure of the true cover of a species. Conversely if data is being collected for purposes of comparison, providing the pin diameter is kept constant from site to site the exaggeration of the percentage cover is not of great importance except where the species tends to have a very high cover value. In the latter instance all areas will show a 100 per cent cover value whereas in fact the true value may range from 70 to 80 per cent in the different sites. If such very abundant species are to be included in a composite study it is necessary to use an optical method.

Percentage cover is a good measure of plant abundance and is very widely used in grassland where it is impossible to define where one individual starts and another ends. The main disadvantage of the method is the rather tedious and slow sampling involved. This can make the measure impractical in a large-scale survey for example. The difficulty in accurately observing the point of the needle in tall vegetation does lead to some error and there is a definite limit to the practicability of the method. The measure can be modified to take into account the stratified nature of the ground layer. The number of times a given species is encountered by a pin is recorded, rather than just the one hit noted in the normal measure of cover. Such a measure, often termed 'cover repetition', gives an estimate of the 'bulk' of plant material and can thus be related to yield (see p. 20). Personal error in the measure of cover repetition tends to be rather high, and if an investigation calls for such a detailed approach it is probably more satisfactory to measure directly the actual weight of plant material in a sample area.

Frequency

The frequency of a species is a measure of the chance of finding it with any one throw of a quadrat in a given area. Thus, if a species has a frequency of 10 per cent then it should occur once in every ten quadrats examined. The measure is obtained very simply by noting whether a species is present or not in a series of randomly placed quadrats. For

example, if 86 quadrats out of a total of 200 contain a given species the frequency is $86/200 \times 100 = 43$ per cent. If a value for the percentage frequency of a species within a single quadrat is required it can be simply obtained by sub-dividing the quadrat into a number of smaller units, then counting the number of sub-divisions within which the species occurs and expressing this as a percentage of the total number of sub-divisions. The results from a series of random quadrats can be finally averaged giving a value often termed local frequency.

Two convenient forms of frequency are used, *shoot frequency* and *rooted frequency* (Greig-Smith 1957). The former is obtained by including as 'present' all parts of the foliage that overlaps into a quadrat; the latter measure only includes a species as present when it is actually rooted within the area of the quadrat. The only advantage of frequency as a measure of abundance lies in the ease and rapidity with which an area can be sampled. Accordingly it has been very widely used as a measure of abundance, often without a realization of the grave disadvantages of the method. The error involved in estimating frequency compared with cover or density is negligible, but the final frequency figure obtained is dependent on several factors, which considerably offset the advantages of speed and facility.

(a) THE EFFECT OF QUADRAT SIZE. It is clear from Fig. 1.7 that quadrats *A* and *B* of different size will give very widely differing frequency values



Fig. 1.7. The dependence of percentage frequency on quadrat size. The two sizes of quadrat (*A* and *B*) will give widely differing percentage frequency values from the same diagrammatic community.

for the species represented in the layout. Quadrat *A* would give a frequency value of about 100 per cent whereas quadrat *B* would give a frequency value in the low intermediate range. Thus, frequency is dependent on quadrat size and it is important to state the size of quadrat used in an

estimate of percentage frequency. Consequently if data are to be compared from different sample plots it is essential to use the same quadrat size throughout.

(b) THE EFFECT OF PLANT SIZE. Again it is obvious that shoot frequency will vary markedly for the two species in Fig. 1.8. Both species have the

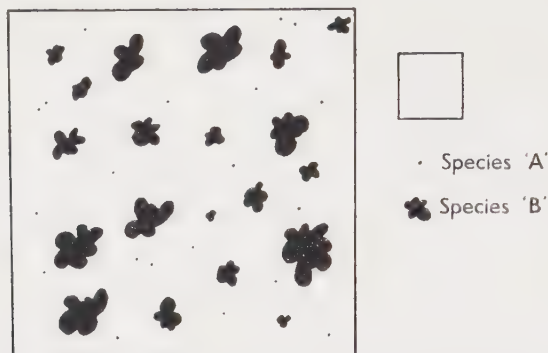


Fig. 1.8. The dependence of percentage frequency on the size of the individuals sampled. Using the quadrat size given, markedly different frequency values will be found though the same number of individuals of each species are present.

same density but, using the size of quadrat shown, species *B* will have a high and species *A* a low percentage frequency. On the other hand if rooted frequency is used both species will have the same frequency value. Again it is essential that the type of frequency measure used is clearly stated.

(c) THE EFFECT OF SPATIAL DISTRIBUTION OF INDIVIDUALS. Three distributions of individuals are shown in Fig. 1.9 all having the same density but a different pattern. With the quadrat size shown the estimated frequency of the species in *A* will be very high, in *B* very low and in *C* intermediate. In *A* the uniform distribution of individuals makes it almost impossible to take a random sample with zero presence, whereas the marked clumped arrangement in *B* gives the other extreme.

It is clear from the above considerations that frequency is not only dependent on the density of individuals but also on several other factors whose effect in any given sample area are usually unknown. Thus, despite the desirability of finding a simple conversion factor for transforming frequency data, which are readily obtained in the field, into density data, the situation is so complex as to make it impossible. Under random conditions it is possible to derive a satisfactory relationship (see Greig-Smith 1957), but random distributions of individuals in vegetation are infrequent and such a transformation is of academic interest rather than practical use.

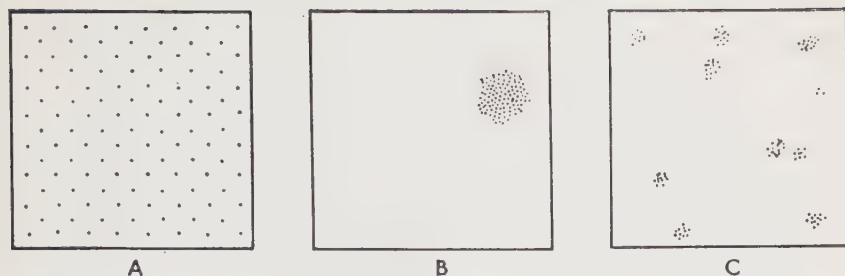


Fig. 1.9. The dependence of percentage frequency on the pattern of the distribution of individuals. With the same number of individuals present in each case and using the same size of quadrat, widely differing values will be obtained from the three communities.

In general, frequency is a useful measure of abundance where comparisons are to be made on a large scale, as long as the limitations are borne in mind but it would seem worth while (despite the time necessary for the sampling) using some other method wherever possible.

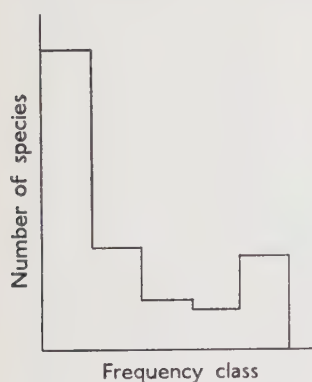


Fig. 1.10. The relationship between frequency class and the number of species falling within each of the classes, showing the typical J-shaped form of the curve.

A further point over which there has been considerable controversy is Raunkiaer's Law of Frequencies often referred to (in its graphical form) as Raunkiaer's J-shaped distribution curves (Raunkiaer 1928). The law of frequency simply states that the numbers of species of a community in the 5 percentage frequency classes, i.e. those of 0-20, 21-40, 41-60, 61-80 and 81-100 per cent frequency are distributed as in Fig. 1.10, i.e.

$$A > B > C \cong D < E.$$

The general fall in the first three or four classes is to be expected since there are more rare species in an area than common ones but the increase in the fifth class (*E*), corresponding to the frequency class 71-100 per cent, is not to be expected and, as Greig-Smith (1957) states, 'It has played a notorious part in some attempts at definition of plant associations'. The increase in class *E* reflects the theoretical infinite range of density and

contrasts with the more strictly defined limits for classes *A*, *B*, *C* and *D*. This fifth class has a possible density range greatly exceeding that occurring in the remainder of the frequency classes *A*–*D*. Accordingly many more species fall into this class, despite the general tendency for 'common' species to be relatively few in number in a community.

Yield

As a measure of abundance, yield has not been used very widely in ecological work. It is determined by clipping a series of sample quadrats, sorting the clippings, drying and weighing them, so that for each species present a figure for dry weight is available. Under field conditions it is very time consuming to sort out clippings into the component species and accordingly its use as a measure of abundance is limited. Where a series of culture experiments or a series of field trials are being undertaken, then yield offers a reliable and absolute measure of both abundance and vigour of a species.

Performance

In some instances it is necessary to know how well a plant is growing in a particular area and a measure of some suitable character can often be made, which reflects the relative vigour or performance, as it is termed, of an individual. Suitable measures include leaf length, leaf width or a ratio of the two, these measures being related to leaf area (the area available for photosynthesis), or flower number, length of flowering spike, number of seeds per capsule, etc., reflecting the reproductive capacity of an individual. The choice of character depends entirely on the species under investigation, but in general leaf length or width is often suitable and gives a good measure of performance. Such a measure was used by Kershaw (1960*b*, 1962*a*) on *Alchemilla alpina* and *Carex bigelowii* (pp. 72 to 74). Phillips (1954*b*) has shown that the ratio of the length of triangulate tip in a leaf of *Eriophorum angustifolium*, to the channelled portion of the leaf, is controlled by the relative growth rates of shoot apex and leaf primordia. As a result this ratio offers a good measure of performance of *Eriophorum*, and its general vigour under different environmental conditions can be readily determined in the field (Phillips 1954*a*).

2 Sampling, Tests of Comparison Application of Quadrat Measures

THE importance of sampling a plant community so as to obtain the maximum amount of information from one set of samples, has been emphasized by numerous workers and Greig-Smith (1957) gives a comprehensive and detailed account of the problems involved. However, it is necessary to outline the more important aspects since a series of conclusions will be based on a single sample, and if the sampling procedure is incorrect, then the derived conclusions may be invalid. The importance of sampling has been stressed to the point where an impression is gained that the procedure is very complicated and in the hands of the uninitiated a dangerous tool. This is only partly true, since the approaches to this problem are all based on common sense. Often the correct procedure and also the one that will give the maximum amount of information on the problem in hand, can be readily devised by careful thought beforehand and with only an elementary knowledge of statistical methods. On the other hand since complex sampling methods are widely used advice from a statistician at an early stage may save wasted labour in the field. The necessity to carefully plan the sampling beforehand is important in yet another sense; recording the contents of a quadrat is nearly always a lengthy and a tedious operation and it is very much better to obtain all the required information from one set of quadrats rather than to have to go back and repeat the sample so as to obtain additional information. Thus no hard and fast rules can be laid down; each sampling procedure should be thought out in relation to a specific problem, the information required being borne in mind.

STATISTICAL METHODS

In all ecological work there is a certain error involved in any field observations or experimental results. This error is partly due to the inadequacies of the equipment, and more important, to an unknown amount of variation always found in biological material. Thus it is necessary to know whether the difference between, for example, the number of buttercups in two plots is a real difference reflecting some variation in the en-

vironment of the two plots, or whether in fact this difference is more than covered by the error attached to the data. In order to assess the reality of the results it is necessary to compare the difference between them with an estimate of the error, or in other words to test the significance of the result.

Normally it is impractical to count every individual present within an area and accordingly a sample of the density is taken from the total population by using a number of randomly placed quadrats.

VARIANCE AND STANDARD ERROR

The following data represents the number of individuals of a species in ten quadrats placed at random in two sample areas:

Plot I	6,	3,	0,	1,	8,	2,	7,	0,	1,	4
Plot II	7,	11,	15,	8,	14,	9,	12,	14,	15,	10

The average density is obtained by summing the numbers and dividing by the number of quadrats in each plot:

$$\text{Plot I} \quad \bar{x} = \frac{S(x)}{n} = \frac{32}{10} = 3.2$$

$$\text{Plot II} \quad \bar{x} = \frac{S(x)}{n} = \frac{115}{10} = 11.5$$

The problem with which the observer is now faced is to decide whether the difference between these two mean values has an ecological significance or whether the sampling error is large enough to explain it. Both sets of data show a range of values reflecting the biological variation of the data and the range (8) is almost equal to the difference between the mean values. It would thus be reasonable to account for the difference in the means by this obvious biological variation. The variation of the density readings is expressed statistically as the *variance* of the sample and is calculated as follows:

$$\text{Variance} = \frac{S(x - \bar{x})^2}{n - 1}$$

This is algebraically identical with

$$\text{Variance} = \frac{S(x^2) - \frac{(Sx)^2}{n}}{n - 1}$$

The latter offers an easier alternative to the rather laborious subtraction of the individual values from the mean value and squaring the results. The divisor ($n - 1$) is known as the degrees of freedom of the sample, and is used instead of n to compensate for using the sample mean instead of the

true population mean. That is to say, if the whole population had been included in the sample, the mean density would be an accurate value. As it is, only ten quadrats were taken and the mean value thus obtained is only an estimate of the true mean, and accordingly the use of this sample mean will slightly bias the estimate of sample variance. By using $(n-1)$, some compensation for this bias is achieved. Usually the degrees of freedom of a sample are one less than the number of samples taken, though there are exceptions to this. The significance of the difference between the two mean values is assessed by comparing it with the standard error of the difference which itself is related to the variance. The calculation is as follows:

$$\begin{aligned}\text{I. } S(x) &= 32 \quad n = 10, \quad \bar{x} = 3.2 \\ S(x^2) &= 6^2 + 3^2 + \dots + 4^2 + 1^2 = 180 \\ S(x)^2 &= 1024 \\ S(x^2) - \frac{(Sx)^2}{n} &= 180 - 102.4 = 77.6 \\ \text{Variance} &= \frac{77.6}{n-1} = 8.6\end{aligned}$$

$$\begin{aligned}\text{II. } S(x) &= 115, \quad n = 10, \quad \bar{x} = 11.5 \\ S(x^2) &= 1401 \\ S(x)^2 &= 13,225 \\ S(x^2) - \frac{(Sx)^2}{n} &= 78.5 \\ \text{Variance} &= \frac{78.5}{n-1} = 8.7\end{aligned}$$

The estimate of the error of the difference between the two means is obtained from the variance of the total data.

Estimate of variance of the total data is given by

$$V = \frac{\left(Sx_1^2 - \frac{(Sx_1)^2}{n_1}\right) + \left(Sx_2^2 - \frac{(Sx_2)^2}{n_2}\right)}{n_1 + n_2 - 2} = \frac{77.6 + 78.5}{18} = 8.67$$

This is the variance of the total data, and the variance of the *difference of the means* accordingly is $V\left(\frac{1}{n_1} + \frac{1}{n_2}\right)$ and the standard error is

$$\sqrt{V\left(\frac{1}{n_1} + \frac{1}{n_2}\right)} = \sqrt{\frac{8.67}{5}} = \sqrt{1.734} = 1.317$$

t-TESTS

The standard error of the difference is now used to assess the difference between the means by a *t*-test:

$$t = \frac{\text{Difference between the means}}{\text{Standard error of the difference}}$$

$$\text{i.e.} \quad \frac{11.5 - 3.2}{1.317} = 6.302 \text{ with 18 degrees of freedom}$$

i.e. the difference between the means is more than six times as great as the standard error of the difference and this difference is highly significant. The level of significance is readily obtained from a table of *t* (Fisher and Yates 1957). With $n=18$ the probability of exceeding a value of *t* of 3.92 by chance is very small ($p=0.001$). Thus with $t=6.3$ the difference between the two mean values arising by chance is very much less than 1,000:1 and this difference is highly significant. [A 5 per cent level of significance (1 in 20) is usually taken as the level of statistical significance.]

It is important to realize that a significant value of *t* does not necessarily mean a real difference between the two values. A large value of *t* can arise either by the difference between two mean values being significant, or by the variance of the two populations being significantly different, or both. Thus it may be necessary in comparing data to use a modified version of the *t*-test when the variance of the two samples is significantly different. This is readily confirmed by a variance ratio test. In the above example the two sample variances were 8.6 and 8.7 respectively and the ratio of the larger variance to the smaller is approximately 1. From variance ratio tables entered with 9×9 degrees of freedom this difference in variance is not significant (a variance ratio of 3.2 has to be exceeded before the difference can be regarded as statistically significant) and the use of a *t*-test is quite legitimate. (For details of the modified *t*-test, see Greig-Smith 1957, Snedecor 1946.)

χ^2 -TEST FOR ASSOCIATION BETWEEN SPECIES, SCATTER DIAGRAMS

Useful information can be obtained from field data on the possible inter-relationships between different species by counting the number of quadrats out of the total in which one or both of a pair of species are found. For example in n quadrats, a contained species *A* and *B*, b species *B* alone, c species *A* alone and d quadrats contained neither species *A* or *B*. A 2×2 contingency table is then made up as follows:

		SPECIES <i>A</i>		
		+	−	
SPECIES <i>B</i>	+	<i>a</i>	<i>b</i>	<i>a</i> + <i>b</i>
	−	<i>c</i>	<i>d</i>	<i>c</i> + <i>d</i>
		<i>a</i> + <i>c</i>	<i>b</i> + <i>d</i>	<i>n</i>

It can be calculated that the number of quadrats containing both *A* and *B*, provided they are not associated in any way, should be $[(a+b)(a+c)]/n$. Thus we have *a* the observed number of quadrats containing both species and we can calculate the expected number assuming an independent relationship between the two species. The other expected frequencies of the different *A* and *B* quadrat combinations can readily be obtained simply by subtraction from the marginal totals. Thus the expected number of quadrats +*A*, −*B* would be

$$(a+c) - \frac{(a+b)(a+c)}{n} \quad \text{and so on.}$$

The number of observed quadrat combinations of *A* and *B* can now be compared with the expected number by a χ^2 -test.

The calculation of χ^2 is conveniently done from the formula

$$\chi^2 = \frac{(ad-bc)^2 \cdot n}{(a+b)(c+d)(a+c)(b+d)}$$

the χ^2 tables are entered with one degree of freedom. The χ^2 value shows whether the difference between the observed and expected numbers of quadrats is significant or merely due to a chance fluctuation. The trend of the association, i.e. whether the association is positive or negative, is given by a comparison of the expected and observed values for the joint occurrence of *A* and *B*. Thus if *A* and *B* occur together *more* frequently than the expected number of joint occurrences, then *A* and *B* are positively associated. Similarly if *A* and *B* occur together *less* than expected they are negatively associated.

The level of association between species is very quickly calculated but since the data is basically a measure of frequency the result obtained is dependent on quadrat size. Consider the relationship of species *A*, *B* and *C* as shown below (Fig. 2.1). Clearly by inspection *A* and *B* are markedly positively associated; *A* and *C* and similarly *B* and *C*, negatively associated. Now consider the effect of sampling in a random fashion such a population with quadrat size 1, roughly equal in size to the individuals *A*, *B* and *C*. Most quadrats would contain either *A* or *B* or *C* or none of them, but hardly any quadrats with *AB*, *AC* or *BC*. Accordingly the χ^2 -test would

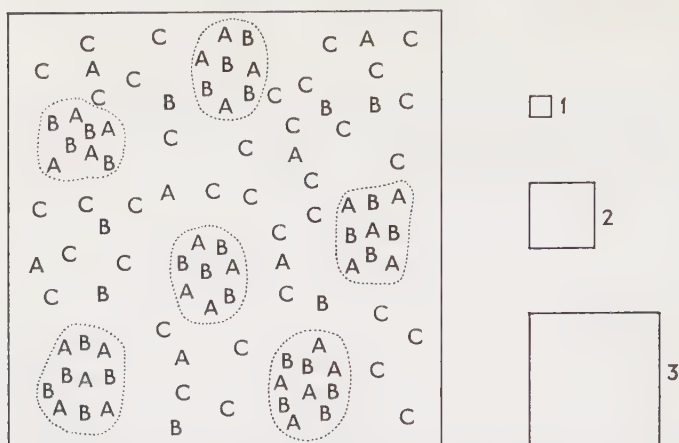


Fig. 2.1. The relationship between quadrat size and trend of association between three species *A*, *B* and *C* (see text).

show strong negative association between all species. With quadrat size 2 *A* and *B* would on the average be found frequently together and species *C* on its own. A χ^2 -test would confirm the obvious trends of association between *A*, *B* and *C*. However consider finally the sampling of the layout with quadrat size 3. Nearly all quadrats would contain species *A*, *B* and *C* and, in this instance, the number of quadrats containing neither of the pairs of species would be zero and χ^2 cannot then be calculated. However, assume the same pattern but with a much lower density of individuals, then the final size of quadrat would show nil association or possibly a positive association between all paired combinations of the three species. It is possible to get three trends of association merely by changing the size of sample quadrat and considerable care must be taken in interpreting a set of positive and negative associations.

Obviously in this instance the pattern of distribution relative to the size of quadrat is important and, since most if not all vegetation contains pattern (see Chapter 7), the trend of association will always vary considerably with different sizes of quadrats. As Greig-Smith (1957) points out, very little attention has previously been directed to this important point and yet it has far reaching effects in the considerations of statistical analysis of community groupings (p. 130). If however the scale or scales of pattern are known, then the variation of trend of association between two species with increasing quadrat size gives valuable information as to the detailed inter-relationships of the species in the area examined.

When data is in the form of a quantitative measure as opposed to mere presence and absence, then a correlation coefficient is a more appropriate

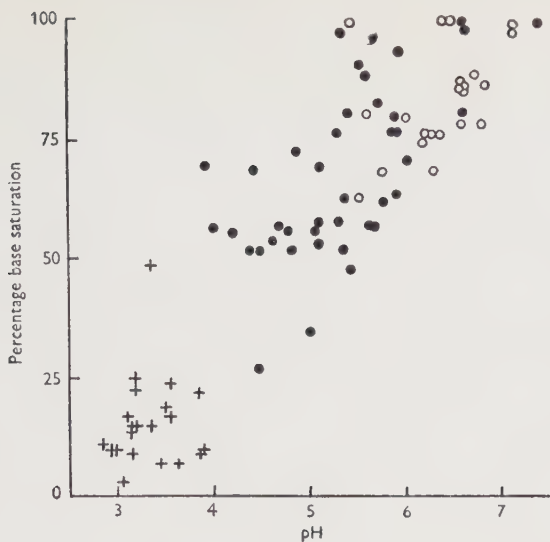


Fig. 2.2. The relationship between pH and base saturation expressed as a scatter diagram. (From Gorham 1953; courtesy of *J. Ecol.*)

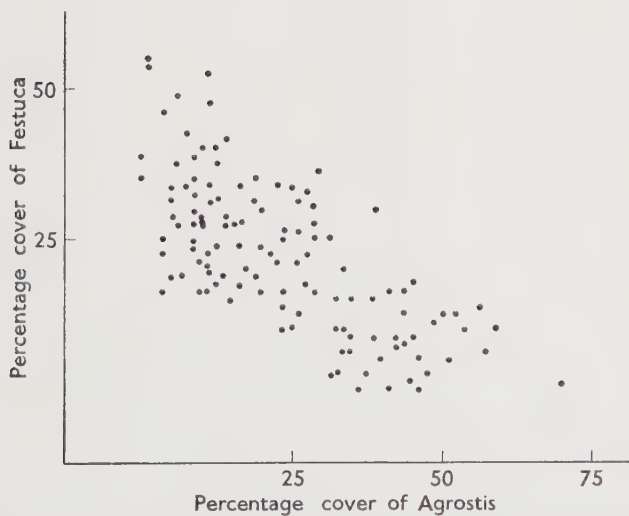


Fig. 2.3. A scatter diagram of the relation between the percentage covers of *Festuca* and *Agrostis* in chalk grassland.

measure of the degree of association; details of the calculation are obtainable in any book of elementary statistics (see also Chapter 5).

An indication of a possible relationship between two factors can be very easily obtained by means of a scatter diagram. An example is given in Fig. 2.2. showing the marked relationship between pH and percentage base saturation. The relationship is so clear-cut that it is probably unnecessary for a correlation coefficient to be calculated; where the scatter of points becomes greater and the degree of correlation correspondingly lower, the visual confirmation of a suspected correlation becomes impossible and it is necessary to calculate the actual coefficient. A scatter diagram showing the relationship between percentage cover of *Festuca* and *Agrostis* in chalk grassland (see also Fig. 2.6) is given in Fig. 2.3, and illustrates a more typical degree of scatter. (The actual data is given in Table 5.1, p. 78.) In most cases it is worthwhile to calculate the correlation coefficient since it can be very tempting to place too much weight on an apparent correlation but one that only has a few degrees of freedom.

SAMPLING METHODS

RANDOM SAMPLING

It is usually necessary to distribute a set of quadrats in an area in such a way that the position of each quadrat is independent of all the other quadrats and is also independent of any prominent feature of the area. This may be made clear by considering the hypothetical case where a series of quadrats are being taken from a sample plot containing a few large and conspicuous thistles. Subconsciously, if not consciously, the very size of the thistles will lead to a feeling that they *really ought* to be included in the sample. If the randomization of the quadrats is being attempted by the closing of eyes or throwing over the left shoulder, then inevitably the tendency is to try to include at least *one* thistle in a quadrat throw. This leads to over-sampling of the area closely adjacent to the thistles. This error is surprisingly common and very often leads to completely biased sampling since the effect of *trying* to make a random throw often produces a final distribution of quadrats which are too regularly distributed. Thus conscious or unconscious prejudgement has to be eliminated, otherwise the final non-random sample will be of little use for further comparison. The use of a *t*-test, or the calculation of any standard error, demands that the original sample should be taken at random. If there has been any introduction of non-random sampling then the calculated standard error is a fictitious figure and a statistical comparison is not valid.

The most satisfactory way of obtaining a random sample from an area is to lay out two lines at right angles to each other to serve as axes; each line is then marked by a convenient number of divisions. A series of ran-

dom numbers taken from tables, (or merely by drawing a set of numbers each time from a pack of cards), then are used as pairs of co-ordinates to locate each quadrat in turn (Fig. 6.1, p. 98). It is often quicker to mark all the random points by a series of pegs before enumerating the quadrats, each peg marking a corner of the quadrat.

Size of sample necessary

It is impossible to make a general rule as to the number of sample quadrats or measurements to take from an area. Each case has to be decided independently and considered against the amount of sampling involved to reach a certain level of accuracy. It is possible to obtain a subjective assessment at least of the size of sample necessary for any given problem. The method consists of taking a sample of five quadrats or readings and calculating a mean value. The number of samples is then increased to 10, 15, 20 . . . and a fresh mean is calculated each time. A graph relating mean value to the sample size is constructed and the point (i.e. the sample size) at which the mean value ceases to fluctuate is easily determined (Greig-Smith 1957). An example is given in Fig. 2.4 for performance data of *Calamagrostis neglecta* expressed as leaf length. The curve

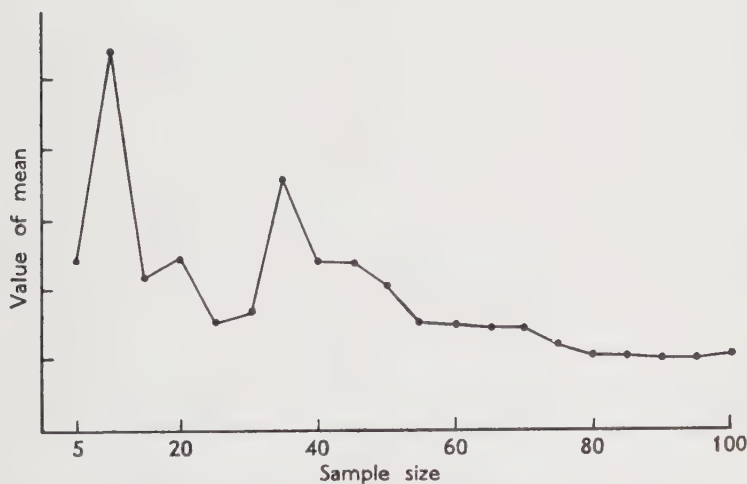


Fig. 2.4. The reduction of the variations in the value of the mean, as the size of sample is increased (see text).

fluctuates considerably up to a sample size of about 50 after which there is little variation and a sample size of 80 would give a reasonably accurate measurement of mean performance in that particular site. (For additional

methods of estimating the required sizes of sample see Greig-Smith 1957, Snedecor 1946, etc.)

It is obvious that as the sample size is increased a better measure of the mean of the population is obtained, but to reduce the standard error the number of samples has to be increased greatly and in general it is recommended to take as large a sample as time will permit. The calculation of a series of mean values as the sample size is increased merely acts as a guide and even if the fluctuations are reduced markedly at a given sample size it does not mean that the fluctuations have ceased altogether. In the case quoted above additional samples would continue to show a slight fluctuation but certainly less than 0.1 mm and since the measurements were taken to the nearest millimetre it would have been pointless to increase the sample beyond 100. Similar considerations can be applied to quadrat density, frequency or percentage cover. However, if very slight differences are suspected to be of ecological significance then a large sample will be unavoidable.

Size and shape of quadrat

If the distribution of individuals in a population is completely random then the size of quadrat used is immaterial except from the standpoint of convenience. Any size convenient for the particular vegetation which is investigated can be used—a small quadrat if the species are small and numerous so that the counting of individuals is made easier, or a large quadrat if the species are large or thinly scattered. However most individuals are not distributed at random and the size of the quadrat has a considerable effect on the variance of the data obtained. This is discussed more fully later (p. 140) but, briefly, if there is a tendency for individuals to be grouped together, the measure of the variance of the data is at a maximum when the size of quadrat is approximately equal to the mean area of the groups of individuals. Since it is usually impossible to predetermine the scale of this pattern (as it is termed) and since such patterns are often repeated on larger scales, the size of quadrat has to be chosen quite arbitrarily. The most suitable quadrat on theoretical grounds being the smallest possible, relative to the type of vegetation and to the practicability of the enumeration of such a quadrat size.

The shape of a quadrat has been a square almost by tradition but some advantages are obtained by the use of rectangular quadrats. Clapham (1932) showed that the variance between rectangular strips was less than between squares of the same area, in one instance at least. Presumably this resulted from a rectangle crossing a high density patch and an adjacent low density patch simultaneously and thus levelling out the variance over the whole area. However, this would not always be true and the only consistent advantage for the use of rectangular quadrats is the increased

facility with which the quadrat can be studied. Thus in large quadrats there is a tendency to crush part of the vegetation by trampling or leaning and this can be a serious disadvantage when several types of measurements are being taken from the same quadrat. One common error associated with quadrat work which is often not appreciated is the 'edge effect'. Frequently a decision has to be taken as to whether a species on the edge is 'in' or 'out' of a quadrat. Where the edge of a quadrat is large relative to the area inside it, this error can be quite marked and thus very long thin quadrats, or conversely very small square quadrats should not be used.

REGULAR SPACED SAMPLES

From the considerations outlined above it is quite clear that in the majority of cases samples of a population taken at random with their resultant standard error are of considerably more use than samples taken at regular intervals. However, there are some exceptions to this general rule. Where data about the abundance of a species along an environmental gradient are required, it is worthwhile to sample systematically along a transect (p. 33) in order to record the abundance of a species in relation to position. Similar considerations apply to isonomes (p. 35) and to the grid analysis of pattern (Chapter 6, p. 96) both of which relate the abundance of a species to location of the quadrats, the former more as a descriptive method, the latter as a statistical analysis of non-randomness. On the other hand regular sampling can lead to a considerable bias of the mean value as would occur in the case in Fig. 2.5. This is a rather extreme

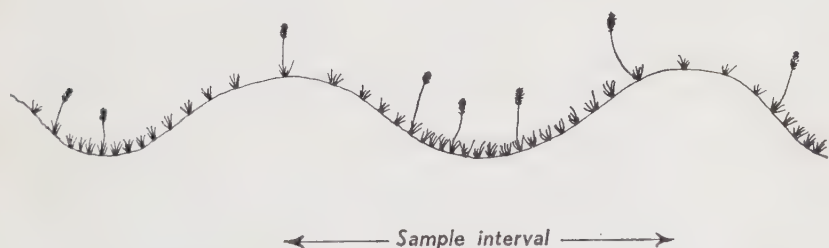


Fig. 2.5. A hypothetical ridge and furrow distribution of a species which when sampled at regular intervals would produce a very biased estimate of abundance.

example of the hypothetical distribution of a species on furrows and ridges which developed in relation to the drainage of a field. The regularly spaced sample points will coincide exactly with the equally regular furrow and ridge, and the mean value for the abundance will be considerably different from that obtained by random sampling.

A similar false impression can be obtained for the optimum level of pH of a species if the sample is not randomized. Thus numerous studies have

been made relating the distribution of a given species to pH by taking a soil sample at each site examined where the species was growing. This in fact is a sample of the variation of soil pH in a given area and the resultant data relates to the frequency distribution of pH in that particular area. Such data offers no real proof of an interrelationship between a species and pH since samples are not randomized, although in fact such a relationship may exist. Emmett and Ashby (1934) present a set of data for *Pteridium aquilinum* and *Vaccinium myrtillus* (Table 2.1) obtained from a

Table 2.1—Frequency distribution of occurrence of *Pteridium* and *Vaccinium* in classes of pH. (From Emmett and Ashby 1934; courtesy of *Ann. Bot., Lond.*)

pH class means	Number of samples	Frequency of <i>Pteridium</i>	Frequency of <i>Vaccinium</i>	Percentage frequency of <i>Pteridium</i>	Percentage frequency of <i>Vaccinium</i>
4.8	2	0	2	0	100.00
4.9	2	0	2	0	100.00
5.0	2	0	2	0	100.00
5.1	5	1	4	20.00	80.00
5.2	13	6	8	46.15	61.54
5.3	17	8	11	47.07	64.71
5.4	7	4	3	57.14	42.86
5.5	44	27	28	61.36	63.64
5.6	78	41	54	52.56	69.23
5.7	16	5	12	31.25	75.00
5.8	7	5	1	71.43	14.29
5.9	9	4	3	44.44	33.33
6.0	7	5	1	71.43	14.29
6.1	3	2	0	66.67	0

random sample. The most frequently occurring pH value in the samples is pH 5.6 and it is not surprising that the frequency of occurrence of *Pteridium* and *Vaccinium* are apparently correlated with this particular soil pH as an optimum for both species. In fact the data merely demonstrates three frequency distributions present in an area which may or, equally well, may not be correlated. The two final columns of the table give the percentage occurrence of the two species, and are derived from the second, third and fourth columns, for example at pH 5.1 one sample out of five contained *Pteridium* which is in fact a 20 per cent occurrence.

The data presented in this form show immediately the dissimilar relationship of each species with pH. It is probably worthy of note that the most efficient way of approaching this particular problem is to take a series of random samples noting the pH and abundance of the species in question. A correlation coefficient can then be readily calculated.

PARTIAL RANDOM SAMPLING

If an area on inspection appears to be heterogeneous, it is pointless to sample at random and to obtain what may be merely an arbitrary set of figures of species abundance. In such a circumstance the recognized method is to sub-divide the area into a convenient number of equal sized areas and to take random samples within each sub-division. If the area proves to be uniform after all then the data can all be lumped together, but on the other hand if the area is variable then information is available which is relative to each sub-division of the plot and is accordingly of considerable interest. The use of partial random samples would be equally applicable to the hypothetical relationship outlined above between the distribution of a species and topography (Fig. 2.5) and the approach in general is ideally suited for sample plots which contain a slight variation of surface topography.

TRANSECT AND ISONOME STUDIES

Transects are of considerable importance in the description of vegetative change along an environmental gradient, or in relation to some marked feature of topography. The method simply consists of laying out a line running across the zones to be sampled and then placing quadrats at known intervals along the line. Various measures can be employed in the description of a transect, density or frequency determinations being made at intervals along the line, and cover determination most conveniently made by using a frame of pins orientated at right angles to the transect at fixed intervals. The data is suitably represented, either by means of a graph or a histogram, of abundance of a species plotted against position on the transect.

In Fig. 2.6 the transect data illustrating the change of composition of grassland on the North Downs is presented; the transect runs from the zone of acidic clay with flints down into neutral or slightly alkaline chalk grassland. The data is in the form of percentage cover, 80 points being taken from each 80 cm strip of the transect and expressed as a percentage. The general distribution of the species in relation to each other and to the slope of the area can be readily appreciated.

A further use of transect studies is in the description of zonation representing stages of a succession and Alvin (1960) gives data on the frequency of different lichen species occurring in different zones of sand-dune vegetation (Fig. 2.7). The sampling in this case was done by dividing the dune system into six zones, 100 quadrats being enumerated in each of the zones. Again the distribution of lichen species is readily appreciated and the general succession from *Cladonia coniocrea*, *C. cornutoradiata*, etc.,

on the first ridge to *C. coccifera*, *C. squamosa*, *C. crispata*, etc., on the third ridge is quite clearly demonstrated.

In general the use of a transect is of greater importance where the variation of vegetation in response to a changing environmental factor is fairly well marked. If the change is only slight it is then necessary to lay out a number of sample plots at intervals along a transect and make a detailed analysis by means of random quadrats, within each plot. By this means slight trends in the density of a species down a slope may be de-

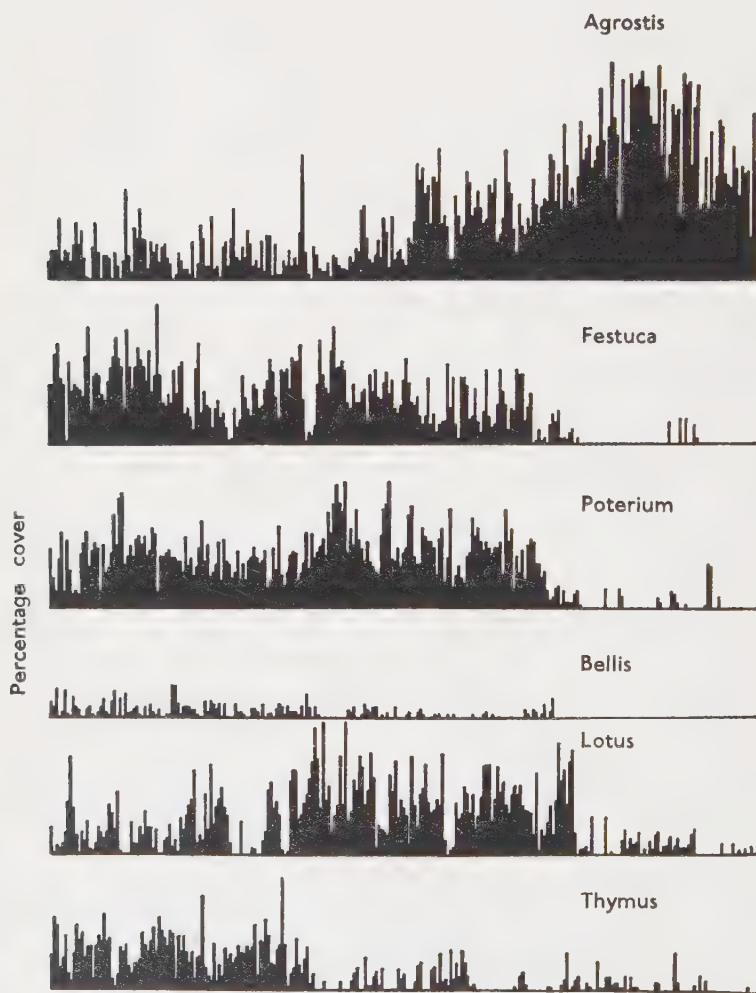


Fig. 2.6. A series of histograms of percentage cover for six species of chalk grassland showing the relationship between the abundance of the species along a transect.

tected and if necessary correlated with environmental factors which are measured at the same time.

An analogous approach to variation in the spatial distribution of a species in a sample plot can be made by the use of the isonome method outlined by Ashby and Pidgeon (1942). The method consists of laying out a grid of contiguous quadrats over a sample area and recording for each quadrat the abundance of the species to be considered. For each species separately the density distribution is then reproduced on squared paper and those squares with approximately equal abundance values joined by a

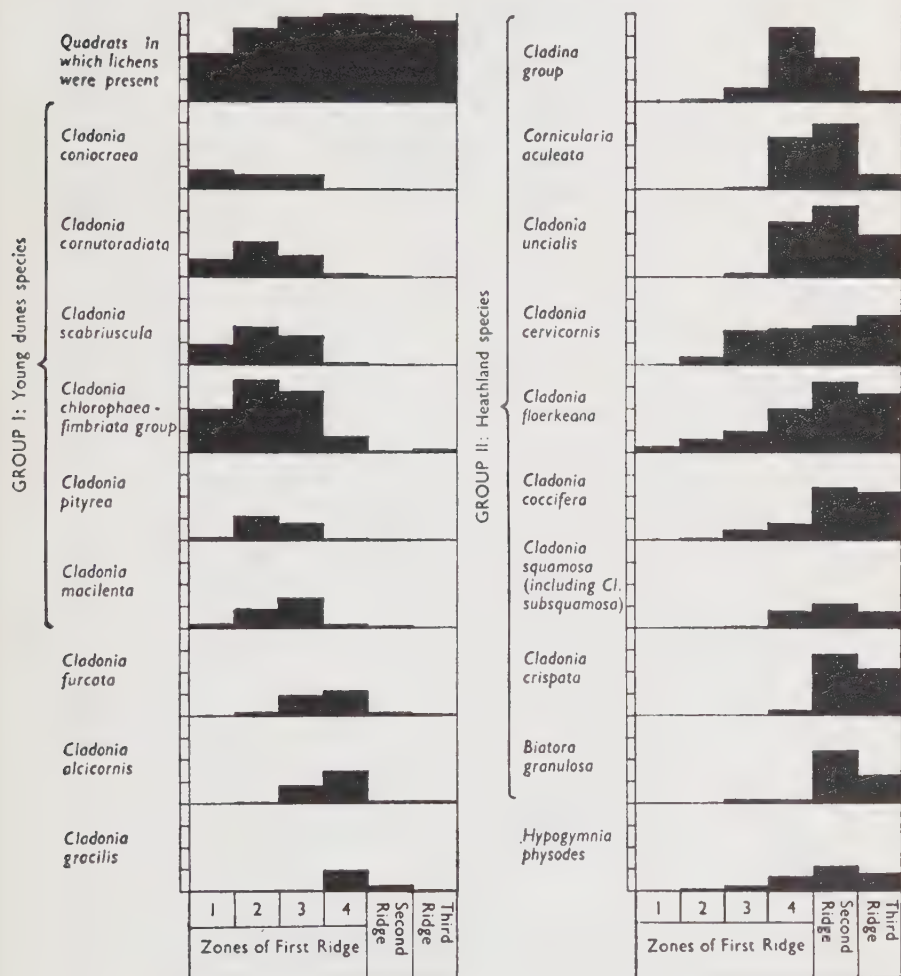
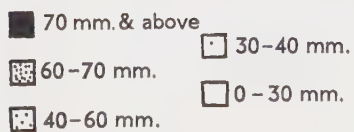
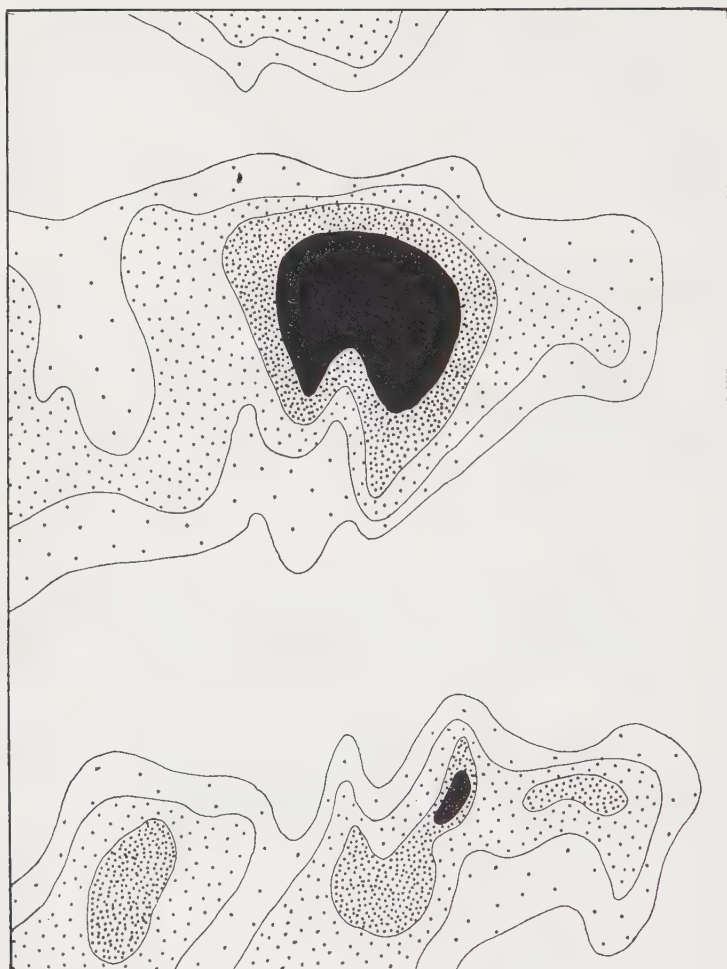
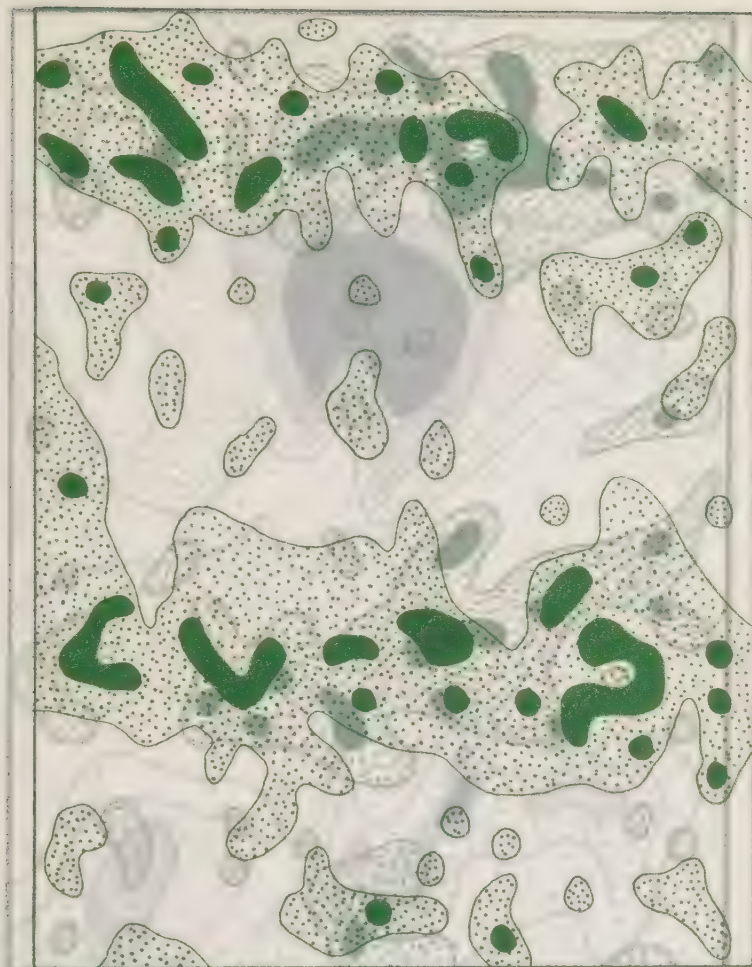


Fig. 2.7. Histograms representing the distribution of the main lichen species in six zones of sand-dune system. One division of the vertical scale represents 25 per cent frequency. (From Alvin 1960; courtesy of *J. Ecol.*)



Topography



■ Density > 2 ▨ Density 2 □ Density 0-1 ■ Density 0-1
 DENSITY OF CAREX FLACCA

Fig. 2.8a. Isolines of the density of *Carex flacca* showing the marked relationship between their relative abundance and micro-topography.

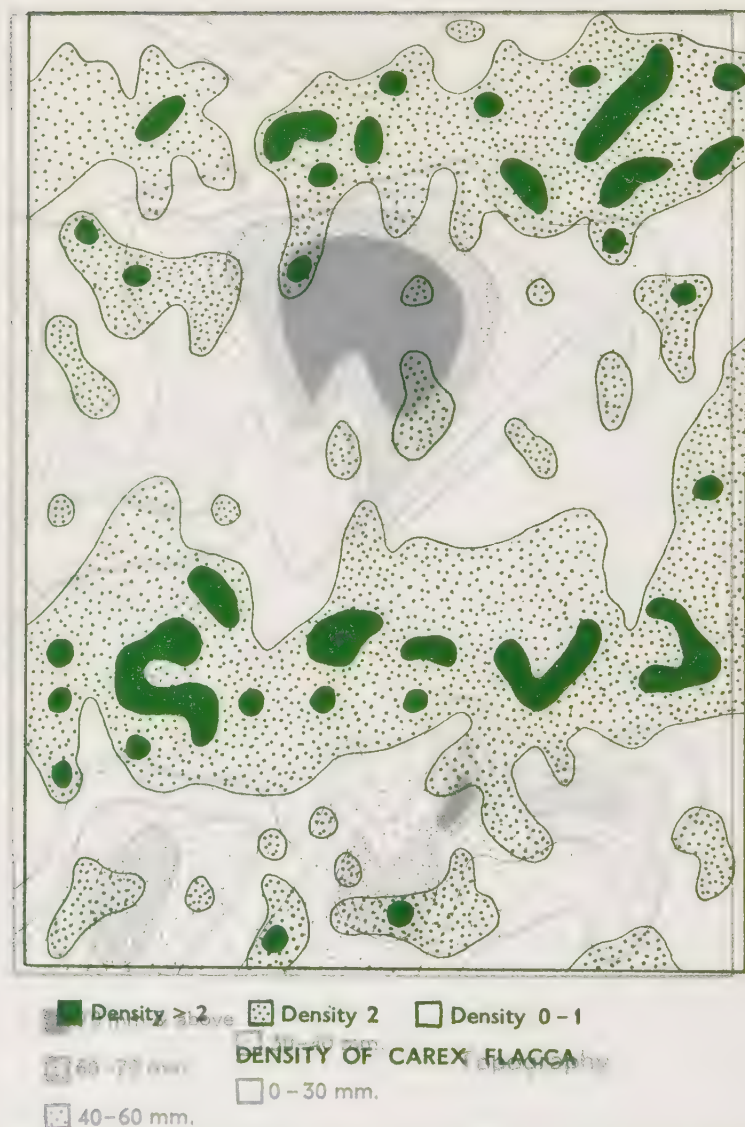


Fig. 2.8a. Isonomes of the density of *Carex flacca* showing the marked relationship between their relative abundance and micro-topography.



Fig. 2.8b. Isonomes of the density of *Carex panicea* showing the marked relationship between their relative abundance and micro-topography.

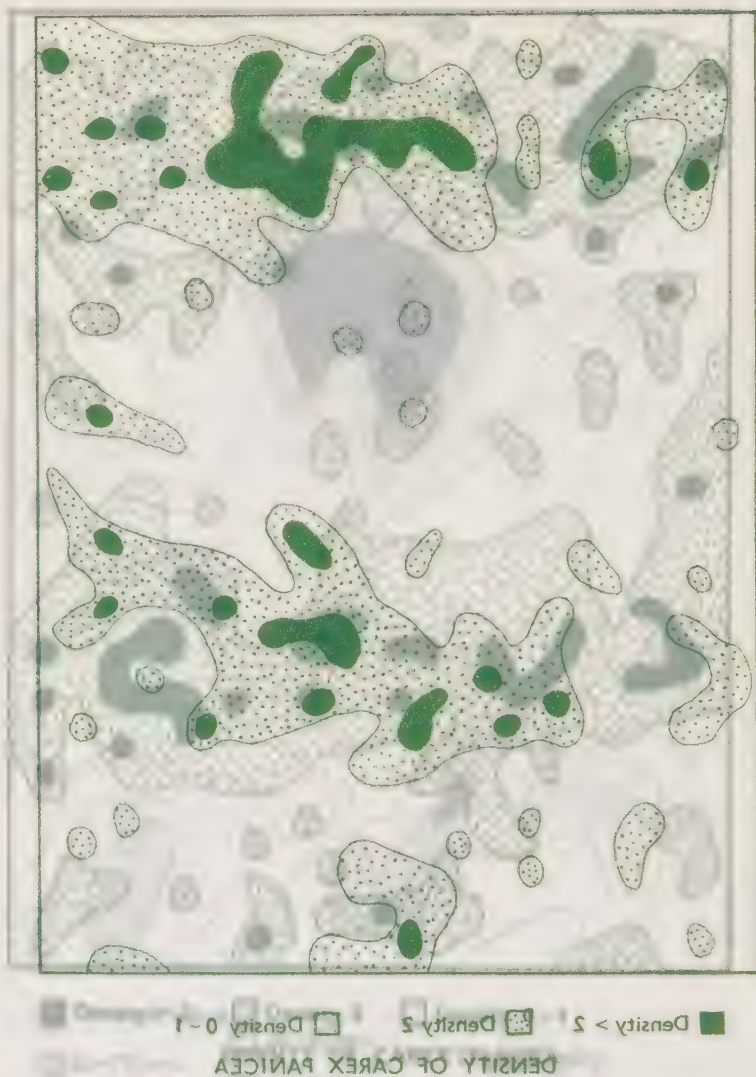
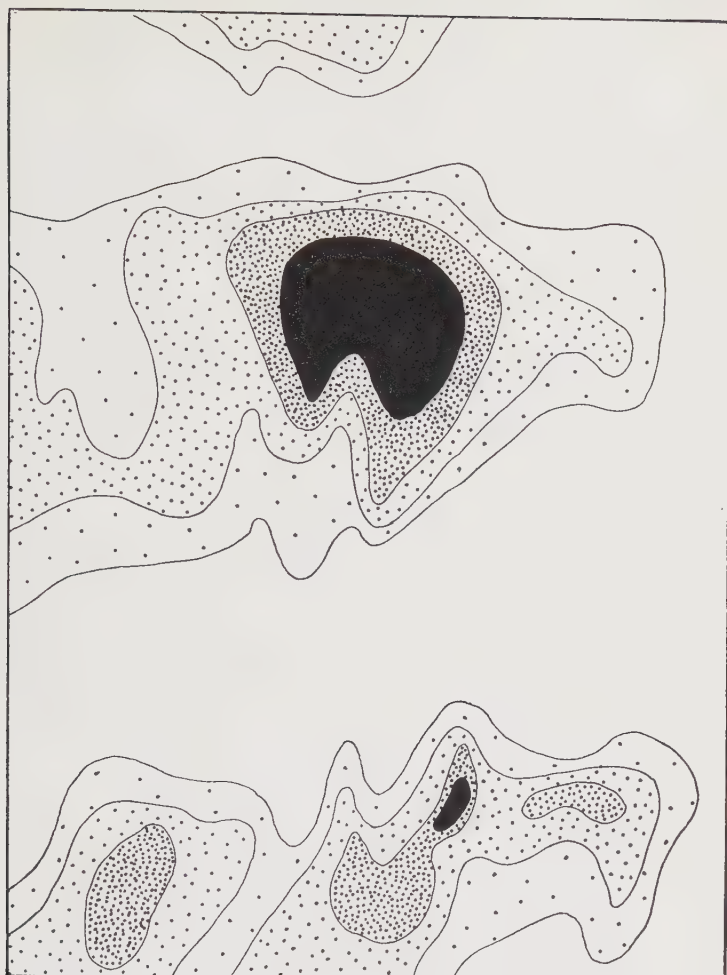


Fig. 2.8b. Isonorms of the density of *Carex panicea* showing the marked relationship between their relative abundance and micro-topography.



■ 70 mm. & above

▤ 60-70 mm.

▥ 40-60 mm.

▧ 30-40 mm.

□ 0-30 mm.

Topography

series of lines, giving a 'contoured' distribution of species abundance. This method can be extended to suitable measurements of the environment so that the distribution of a species in an area can be related to the distribution of other species or to environmental factors. The method may be made clearer by considering an actual example.

The microtopography of an area of hummocks in limestone grassland at Malham Tarn, Yorkshire, is presented in the form of an isonome (Fig. 2.8) constructed from a series of height measurements taken from a levelled datum line. At the same time the density of *Carex flacca* and *C. panicea* were recorded for each unit of the grid and the corresponding isonomes constructed from the density data for both species. The marked relationship of both *Carex* species with the hollows, is readily appreciated and the isonome method is in general a very convenient way of depicting relationships between species or between a species and some environmental factor. Clearly the method is only applicable where the distribution of species varies quite markedly; where the distribution is not readily appreciated by the visual inspection of an isonome it is necessary to use a more elaborate method (see Chapter 6).

Both transect and isonome methods illustrate the use of regularly spaced samples in describing an area and it should be again emphasized that the sampling procedure most suitable for a given problem is usually chosen or designed for that individual problem. The choice of measure, the size of quadrat, the size of sample and the random or regular position of the quadrats can all be decided more by common sense than resorting to complex statistical theory.

3 Vegetational Change. Plant Succession and the Climax

SUCCESSION

AN area of bare ground when stripped of its original vegetation by fire, flood or by the drainage of a lake, does not remain devoid of vegetation for very long. The area is rapidly colonized by a variety of species which will subsequently modify one or more environmental factors. This modification of the environment in turn allows further species to become established. A subsequent development of the vegetation, by this reaction of the vegetation on the environment followed by the appearance of fresh species, is termed *succession*. The concept of succession was largely developed by Warming (1896), and Cowles (1901) who related the stages of sand-dune development in a time series, and finally by Clements (1904) who outlined in considerable detail the stages of a large number of plant successions, initiated by a variety of factors (Clements 1916).

Clements introduced the term *sere* to describe the developmental stages through which the vegetation passes until it reaches an ultimate state of equilibrium with the climate and major geological factors of the area. Thus the well known colonization of open water is termed the hydrosere and includes several marked *stages*, starting with submerged aquatic plants and followed successively by floating-leaved aquatic plants, reed swamp, marsh or fen and finally carr. Clements similarly termed the stages of salt marsh succession a halosere, sand-dune succession a psammosere and the development of vegetation on bare rock surfaces a lithosere.

Analysis resolves the process of succession into several important phases :

1. Nudation, which is the initiation of the succession by a major disturbance in the environment.
2. Migration of available species (migrules) to fill the vacant ecological niches.
3. Ecesis or the subsequent ability of the migrules to germinate, grow and reproduce successfully.
4. Competition.
5. Reaction.
6. Final stabilization. (Clements 1916.)

The reaction of species on the environment is one of the outstanding features of succession and constitutes the major mechanism of environmental change which allows further migrules to enter. A very obvious example of such a reaction is found in the formation of sand-dunes. The

establishment of a rhizome fragment of *Ammophila arenaria* and the subsequent production of aerial shoots constitutes a disturbance of the environment at that point. The aerial parts offer an increased impedance to the wind, any sand particles carried by the wind being deposited round the plant and gradually burying it. As the sand accumulates, continued growth of the *Ammophila* keeps it at a generally higher level than the low mound that is formed, and accumulation of wind-borne sand continues. Production of axillary buds and the development of the typical clumped habit of *Ammophila* accelerates the rate of 'dune' formation and gradually over a period of years the dune gets progressively larger (Fig. 3.1). This is a very

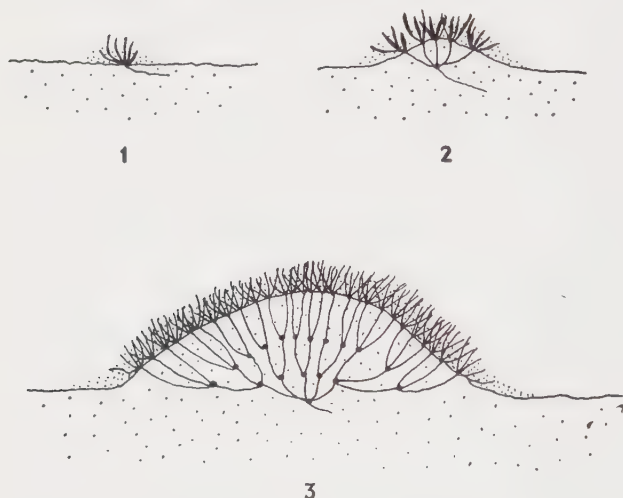


Fig. 3.1. Dune formation by the gradual deposition of wind-carried sand particles around the aerial shoots of *Ammophila arenaria*.

marked example of reaction of a plant on the environment and is comparable to the increase in the rate of silting of a lake by the early colonisers, which constitute the first stage of a hydrosere. The same mechanism operates, that is increased impedance to water-borne particles. These are deposited around the vegetative parts of the plants. The depth of water decreases over a period of years until other species with their vegetative parts above water begin to invade. The rate of silt accumulation (plus vegetable remains from the plants themselves) increases and opens the way to the gradual development of reed swamp and then fen vegetation.

These two examples of reaction are fairly obvious, but frequently the reactions which are contributing to the impetus of what is clearly succession are far from clear. Vegetational change was divided by Clements into two kinds: *Primary succession* initiated on a bare area where reactions are,

initially at least, often fairly clear, and *Secondary succession* initiated by a major environmental disturbance and disrupting a previously initiated succession or producing a marked modification in stable vegetation. For example removal of grazing from grassland, or a forest fire, both initiate a secondary succession and it is in such examples of succession that reactions are often very obscure. It may be that ecesis and competition play a more decisive role in such instances.

Other classification systems have sub-divided secondary successions into a varying number of divisions, but in general little is gained by a complex classification of successions.

The direction in which a succession will develop has been argued at considerable length in ecological literature. Phillips (1934) states 'Succession is *progressive* only; all examples of apparent retrogression are explicable in terms of some disturbing agency'. Similarly *true* succession is defined by Michelmore (1934) as inherent succession of the vegetation which takes place through the plants altering their environment. This is to be distinguished from physiographic succession due to an initial change in the environment which should apparently not be included. Similarly Tansley (1916, 1930) employs the terms autogenic and allogenic to distinguish between these two distinct successional causes. For an understanding of succession at a level which serves as a *useful* concept, such a degree of fine definition is not essential. Any *directional change* in vegetation, be it due to intrinsic properties of the plants, or to changing extrinsic factors (the environment), gives a useful and workable definition of succession as a dynamic process. This was admirably expressed by Cooper (1926) who stated that 'Succession is the universal process of change which is embodied in the great vegetational stream; all vegetational changes, whether internally or externally induced, whether gradual or abrupt, are therefore successional.' (See also Gleason 1927.)

Numerous examples of succession have been described in detail, but very few cases are available where the succession is related to even an approximate time scale. One or two outstanding exceptions to this have appeared in the literature, notably colonization of glacial moraines in Alaska where the age of the moraines is known with a fair degree of exactness. This enables the plant succession and attendant modification of the substratum by the vegetation to be related to a time scale. Similarly the sand-dune succession in the Michigan Lake Basin in America has been studied in detail and related to a time scale obtained by radio-carbon dating methods.

The Glacier Bay region in south-east Alaska is typical of the large-scale glacial retreat that has occurred over the last 200 years in North America, Europe and Scandinavia. The position of the snout of the glacier in historic times can be estimated by growth ring counts of the present spruce forest. Thus ring counts of trees growing beyond the maximum extent of glacier activity (easily recognized from aerial photographs) show the oldest trees to be over 600 years of age and growing on a 'raft' of fallen submerged trunks. The oldest trees on the last morainic ridge are approximately 200 years old, whilst the maximum age of trees on moraines nearer the present site of the glacier progressively decreases. Cooper (1937), Field (1947) and Lawrence (1953) all contributed to a detailed study of the recession of the glacier and a clear picture is now available (Fig. 3.2).

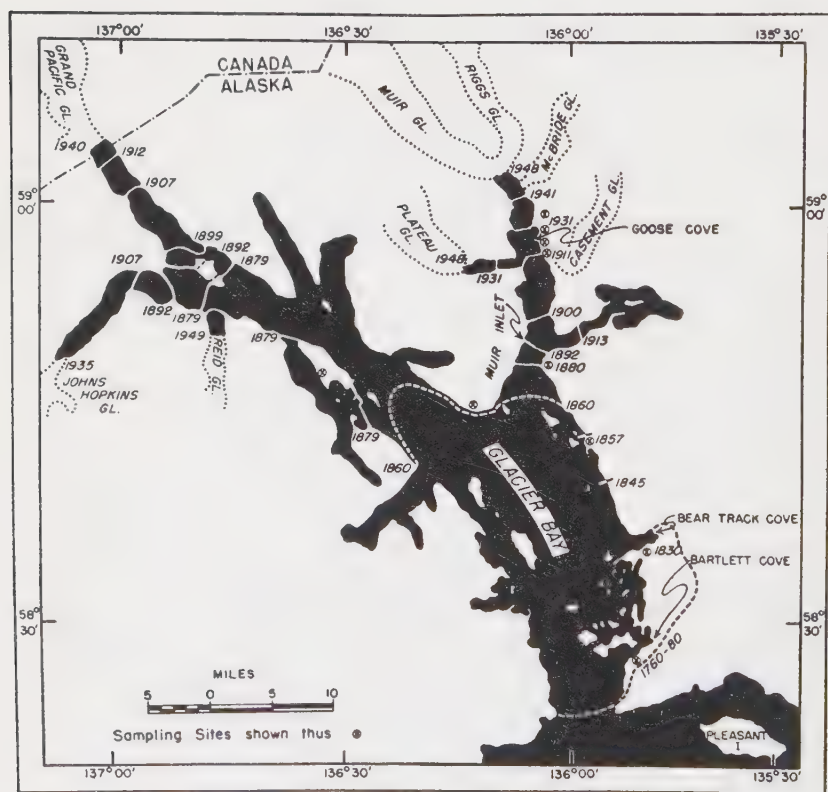


Fig. 3.2. The Glacier Bay fiord complex showing the rate of ice recession.
(From Crocker and Major 1955; courtesy of J. Ecol.)

Their findings are confirmed by comparison of written records extending back to the 1890's and photographic surveys commenced around 1916.

The stages of succession have been described by Cooper (1923, 1931, 1939) and by Lawrence (1953). The pioneer stage is characterized by *Racomitrium canescens* Brid., *R. lanuginosum* (Hedw.) Brid., *Epilobium latifolium* L., *Equisetum variegatum* Schleich., *Dryas drummondii* Rich. and *Salix arctica* Pall. The next stage is the appearance of *Salix barclayi* And., *S. sitchensis* Sans. and *S. alexensis* (And.) Colville, which start as prostrate forms eventually developing an erect habit and forming dense scrub. *Alnus crispa* Ait. Pursh. dominates the next stage of the succession and eventually forms almost pure thickets (with some scattered individuals of *Populus trichocarea* T. and G.), which are finally invaded by *Picea sitchensis* Carr. *Picea* initially forms pure stands, but over a period of time

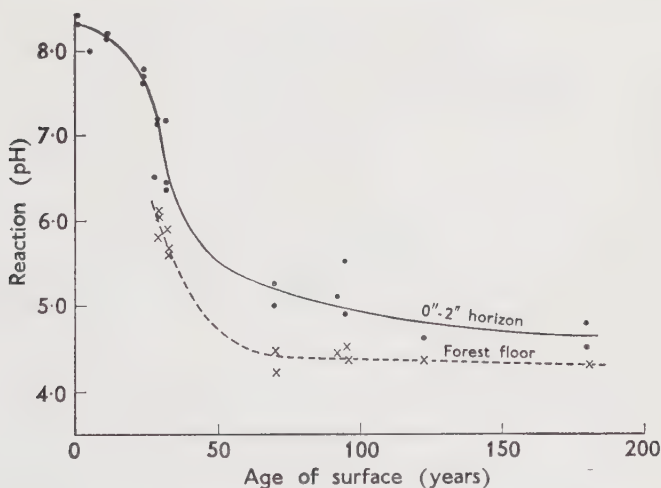


Fig. 3.3. pH of litter residues and surface horizons of the mineral soil with increasing age of surface. (From Crocker and Major 1955; courtesy of *J. Ecol.*)

Tsuga heterophylla Sarg. and *T. mertensiana* Carr. enter the community. On well drained slopes this stage represents the climax vegetation of the area. However, where the ground is gently sloping or flat *Sphagnum* species subsequently invade the moss mat of the forest floor and through the growth of *Sphagnum* and its ability to retain large amounts of water, the forest floor becomes soggy and root aeration decreases. This leads to the elimination of the tree species and to the establishment of muskeg dominated by *Sphagnum* species, with occasional scattered individuals of *Pinus contorta* Laws, which can apparently tolerate the wet conditions which prevail.

Crocker and Major (1955) have studied the time sequence of this succession and the reaction of each stage on the properties of the soil. In the earliest stages of soil development following glacial recession the processes involved appear to be greatly affected by the type of vegetational cover.

The reaction of the soil parent material is quite high with a pH of 8.0-8.4, due to the occurrence of marble in the geological formations of the area. The soil pH falls rapidly with the establishment of the vegetation (Fig. 3.3) and furthermore the rate of increase of acidity is markedly affected by the type of vegetational cover. Bare surfaces show almost no change of pH over a 30-year period, while *Populus*, *Dryas* and *Salix* sites show a more marked decrease of pH, and *Alnus* produces a striking acidifying effect, lowering the pH of the surface soil from about 8.0 to 5.0 in 30-50 years (Fig. 3.4). This rapid decrease of pH ceases with the invasion

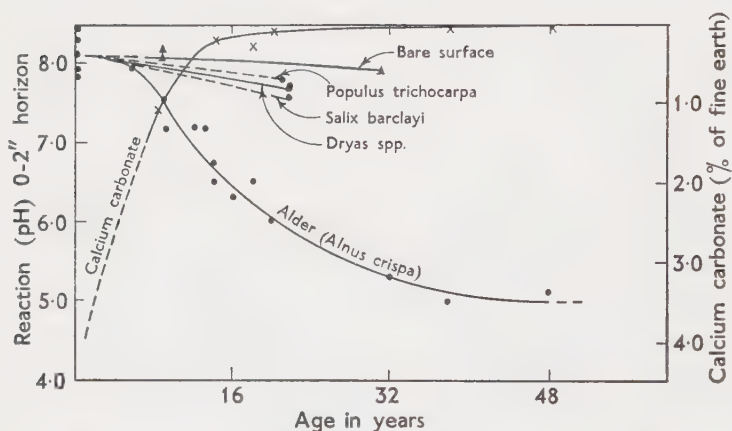


Fig. 3.4. Rate of change of pH in 0-2 in. horizon relative to different vegetational cover and rate of calcium carbonate change under *Alnus*. (From Crocker and Major 1955; courtesy of *J. Ecol.*)

of *Picea*, the leaf litter of this species appears to be approximately of equal acidity to *Alnus* and has no significant effect on the mineral soil.

The organic carbon and total nitrogen concentration in the soil shows equally marked change with time (Figs. 3.5 and 3.6). The vast increase of soil nitrogen is related to the presence of bacterial nodules on the roots of *Alnus* which actively fix atmospheric nitrogen and contribute largely to the reserves of nitrogen in the soil via leaf fall (Fig. 3.7) (Lawrence 1958). The invasion of spruce at this stage and the subsequent reduction of soil nitrogen strongly suggests this to be the important consideration controlling the time of entry of the spruce into the alder thickets. The

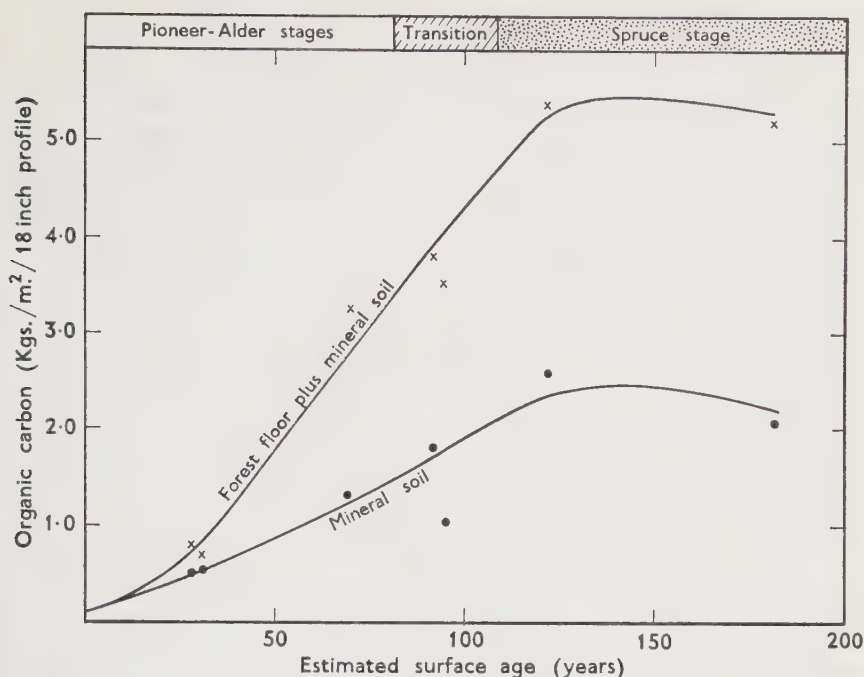


Fig. 3.5. Organic carbon accumulation in mineral soil and forest floor. (From Crocker and Major 1955; courtesy of *J. Ecol.*)

elimination of the alder and its root nodules decrease the net annual addition of nitrogen as leaf litter, for spruce has no such root structures and accordingly the soil nitrogen is reduced.

The complete succession from bare morainic detritus to mature spruce forest takes approximately 250 years during which time the most significant reaction of the vegetation appears to be the building up of soil nitrogen. The reduction of soil pH is probably also closely related to this. The building up of organic carbon will influence to a considerable extent the development of soil structure and will lead to a soil with 'crumb-structure' which is markedly different from the rather amorphous glacial till. In turn this will affect soil aeration and movement of water in the soil, and both of these factors probably influence the succession. However, very little data is available which would enable a general assessment of the effect of such factors on vegetation apart from the rather more obvious relationships that exist. Clearly a detailed study is required of the exact environmental requirements of each species contributing to the succession before the complete mechanism of the succession can be fully appreciated.

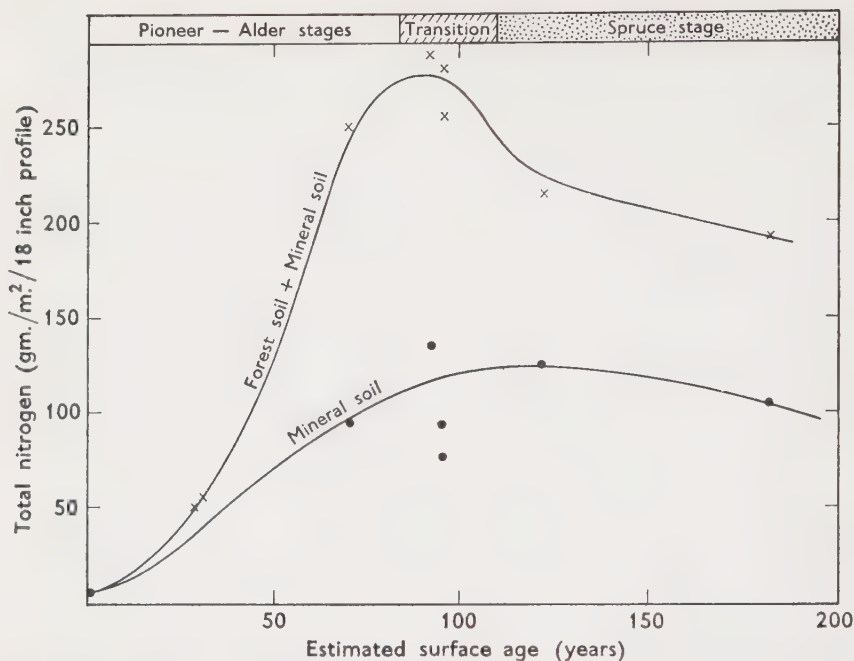


Fig. 3.6. Change of total nitrogen content of soils on surfaces of varying age. (From Crocker and Major 1955; courtesy of *J. Ecol.*)

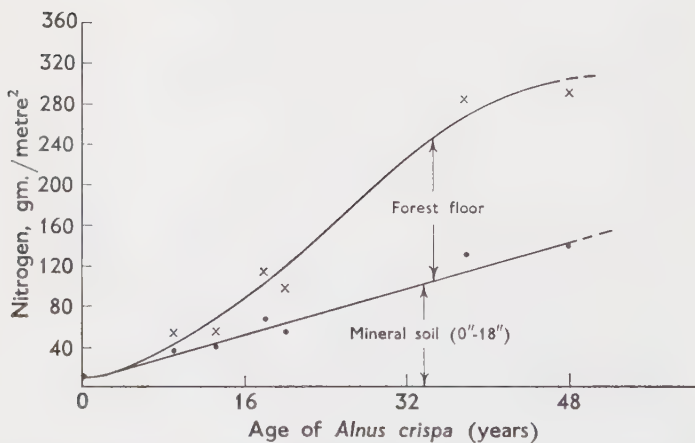


Fig. 3.7. Accumulation of nitrogen in the mineral soil and forest floor under *Alnus crispa*. (From Crocker and Major 1955; courtesy of *J. Ecol.*)

LAKE MICHIGAN SAND-DUNE SUCCESSION

Cowles' (1899) classic description of the sand-dune vegetation of Lake Michigan was one of the early contributions to the concept of plant succession. More recently Olson (1958) has re-examined the successional stages in this area in relation to both the development of the soil and to the age of each dune system.

During and after the retreat of the ice-age glaciers from the Great Lakes region the resultant fall in the general level of the lakes left several distinct 'raised beaches', with their associated dune systems. These systems, running parallel to the present shore line of Lake Michigan are about 25, 40 and 55-60 ft above the present level of the lake. These old dune systems have all been dated recently by radio-carbon methods and the highest system above the present lake level (Glenwood) turns out to be slightly over 12,000 years of age. The more recently established dunes were aged by morphological studies of the *Ammophila* colonizing them and growth ring counts of *Pinus banksiana* which enters the succession at an early stage (Fig. 3.8).

The pioneer stage of the succession is dominated by *Ammophila breviligulata* which occasionally becomes established from seed but normally invades freshly deposited sand by rhizomes from young previously established dunes. The rate of dune formation established from a morphological examination of *Ammophila* is rapid and stable dunes are formed in about 6 years. Dunes which have been established for 20 years or more, still have *Ammophila* but with an obviously reduced level of vigour. This loss of vigour has been related to potential leaching of nutrients over a 20-year period. Another suggestion invokes the inherent tendency of this species for internodal elongation which does not cease completely when stabilization has been reached. This results in the growing apex being pushed into the dry surface layers of the sand which are unfavourable for plant growth, with the consequent reduction of vigour of the plant as a whole. A further possibility may be found in the average age of the plants themselves, the loss of vigour being due to the slowing down of physiological mechanisms, resulting directly from old age (see Chapter 4, p. 63). The next stage of the main line of succession is the arrival of *Pinus banksiana* and *P. strobus* which enter immediately dune stabilization is reached. These species eventually are replaced by the final stage dominated by *Quercus velutina*. This main succession is summarized in Fig. 3.8 together with the modifications present in those dune systems where local variation of the environment can change the course of the succession markedly. Thus damp depressions caused by impeded drainage develop into a grassland community and, on the other hand, sheltered pockets on the lee slopes progress to a *Tilia americana* dominated intermediate stage.

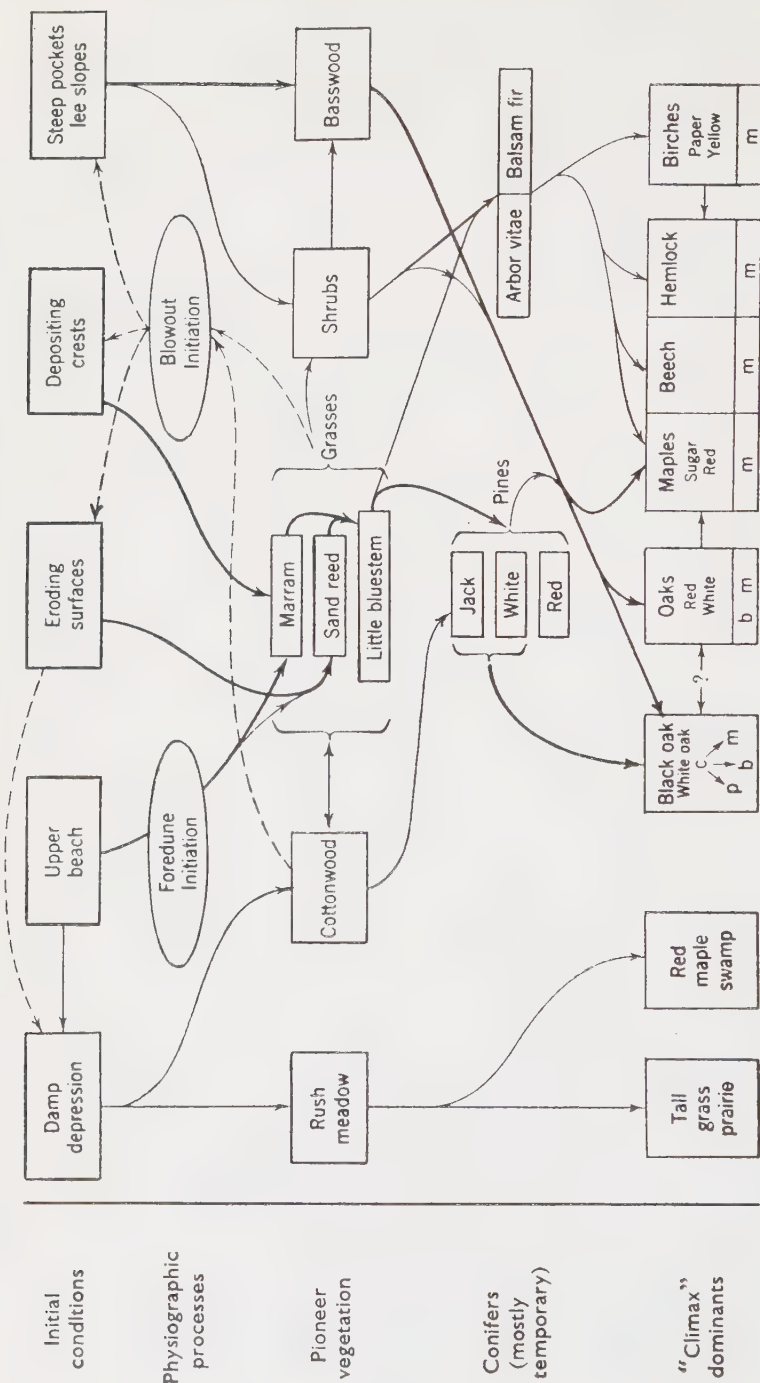


Fig. 3.8. Schematic alternative dune successions in the Lake Michigan dune systems. (From Olson 1958; courtesy of *Bot. Gaz.*)

This different course of succession is related, in part at least, to the microclimate of these pockets which are largely protected from excessive solar radiation and wind effects. Accordingly moisture availability will be higher, which in addition to the obvious relation to plant growth would contribute some protection from fires which occur frequently in the area, the relatively moist pockets tending to be by-passed. In addition these dune pockets tend to accumulate fallen leaves brought in from the more exposed parts of the dune system and the general nutrient status of the soil increases at the expense of the rest of the area. The reaction of the vegetation on the properties of the soil is broadly similar to the example discussed above but the rate of change is considerably slower. The leaching of carbonate from the soil is very rapid (Fig. 3.9) and the surface layers (10 cm) are more or less devoid of carbonate from the soil after a few hundred years. There is a slow building up of organic carbon (Fig. 3.10) and soil nitrogen (Fig. 3.11). These three environmental changes are virtually completed in 1000 years and subsequent generations of *Quercus* have little effect on these soil properties.

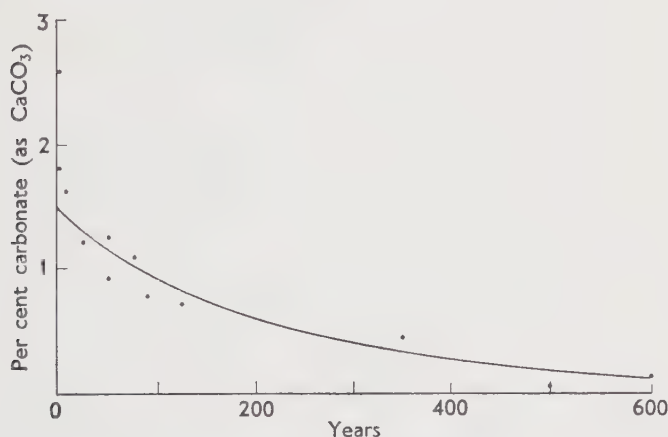


Fig. 3.9. Leaching of carbonates from the surface layers of dune soil. (From Olson 1958; courtesy of *Bot. Gaz.*)

Again the relationships between the environment, the vegetational stages and the development of the succession through modification of the environment can only be described in a general way. The initial dune formation is clear and results in an ecological niche with low fertility which is in fact invaded by species with low nutritional requirements. The subsequent accumulation of soil nitrogen and organic carbon presumably control to some extent the time of entry of oak into the succession. What evidence

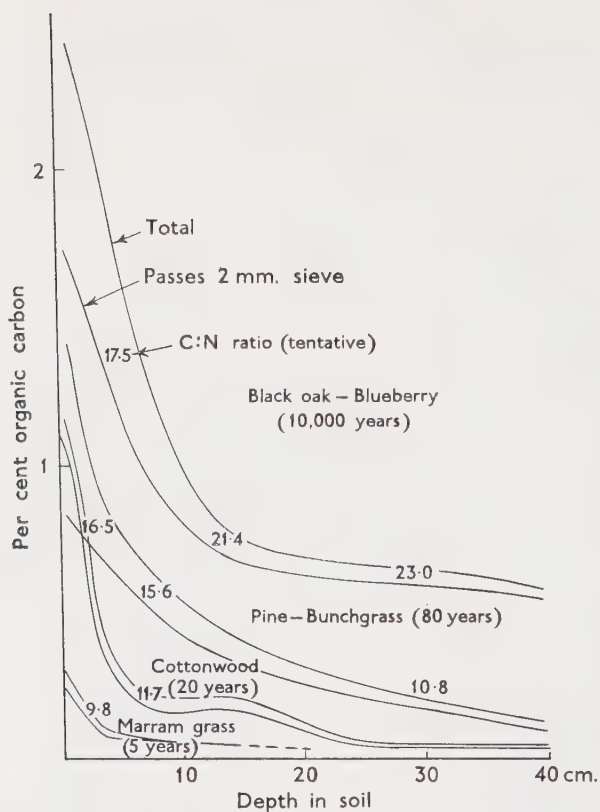


Fig. 3.10. Selected profiles of organic carbon from four dunes of contrasting age. (From Olson 1958; courtesy of *Bot. Gaz.*)

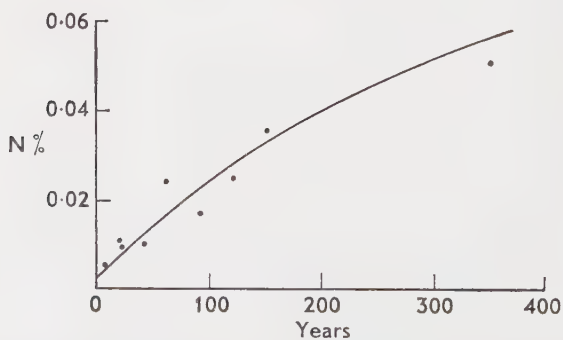


Fig. 3.11. Increase of soil nitrogen in surface layers of soil from dunes of different age. (From Olson 1958; courtesy of *Bot. Gaz.*)

there is suggests that *Quercus velutina* has relatively low nutrient requirements and accordingly able to thrive in a habitat which remains at a very low level of soil fertility. The annual addition of leaf litter from the final stages of the succession appears to be equivalent to the amount of nutrient required to maintain the *Quercus* communities. Thus the soil conditions remain fairly constant over a long period of time (probably an indefinite period) and limit the further development of the succession. It appears very improbable that species with higher nutrient requirements will ever enter the succession and the occasional and isolated hickory, beech and maple trees are restricted to sites with special topographic or drainage features. Accordingly the *Quercus velutina* represents the final stable vegetation of the area largely restricted by the edaphic features outlined above.

THE CLIMAX STATE

In both the examples of succession described above the vegetation has developed to a certain stage at which point it has reached a state of equilibrium with the environment. This final stage of the succession is related directly to the environment and is referred to as the climax. Numerous definitions of the climax have been made: Braun-Blanquet (1932) defined it as the development of vegetation and the formation of soil towards a definite end point determined and limited by climate. Similarly Odum (1953) suggests that a climax is the final or stable community in a successional series; it is self-perpetuating and in equilibrium with the physical habitat. Both these definitions seem very similar and the differences do not appear to be completely incompatible. However, they reflect the outlook on climax vegetation of two schools of thought which have developed since the initial usage of the word in an ecological context. The two theories concerned are referred to as the monoclimax and the polyclimax theories which respectively relate the control of climax vegetation to one factor, that of climate, or to a number of factors ranging from climate to less obvious edaphic or even biotic (i.e. animal) factors.

The existence of stable communities largely controlled by edaphic factors are obviously not denied by the protagonists of the monoclimax theory but they are regarded rather as 'exceptions' and categorized by the introduction of special terms—'subclimax' and 'post-climax' for example (see below). [Whitaker (1953) lists and describes in detail the numerous terms used in relating edaphically controlled climax vegetation to the ultimate climatic climax.] It is claimed that over a long period of time these apparent exceptions will be completely modified by the action of the climate into true climax vegetation.

The polyclimax theory is not hampered by this necessity of introducing

a large number of terms to describe apparent exceptions to the theory—an edaphic geological or physiographic climax is accepted for what it is.

The monoclimax theory was developed largely by Clements (1916) and some of the terms relating to climax vegetation clearly show the inherent difficulty of defining a time scale over which stability can be assessed.

Subclimax

This is the penultimate stage of a succession which persists for a long time but is eventually replaced by the true climax vegetation. For example, Gleason (1922) and Cooper (1926) give an account of the relic coniferous forest uncovered in the city of Minneapolis and which was shown to be immediately post-glacial. The present climax is deciduous forest which presumably has very slowly replaced the coniferous 'subclimax'.

Disclimax

This is the vegetation replacing or modifying the true climax after a disturbance of the environment. The majority of 'natural' grasslands in the British Isles below 1500 ft are maintained by the grazing of cattle and sheep, and if this factor was removed it is believed that a deciduous forest climax would result. Similarly the introduction of prickly pear cactus in Australia has formed a disclimax over wide areas.

Post-climax and Preclimax

Climatic areas, latitudinally zoned from the equator to the arctic, are not discontinuous. There is a gradual change from one zone to the next reflected in equally gradual vegetational change. Any slight fluctuation of climate will modify the vegetation and such vegetational differences reflecting cooler and/or moister conditions than the average (usually topographically induced) are termed post-climax, drier and/or hotter, pre-climax.

The monoclimax theory and the excessive use of this type of terminology has been severely criticized by many ecologists since rather than clarifying the position the dozens of special terms complicate the issue out of all proportion. Conversely an explanation by polyclimax theory is readily available.

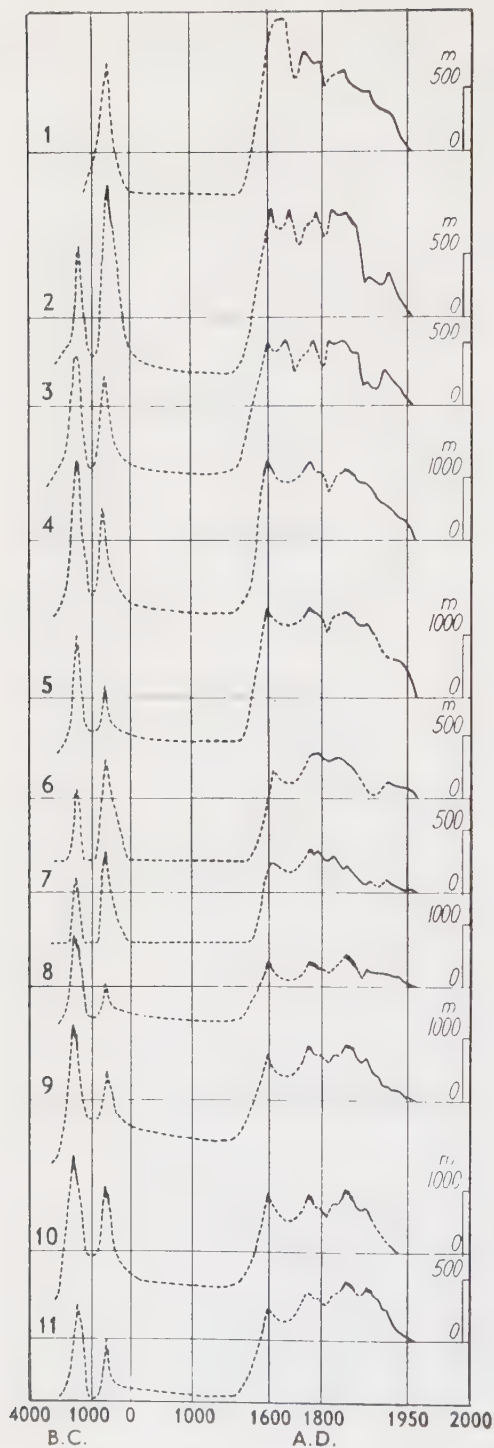
The real difference between these two schools of thought lies not in the possible existence of edaphically-stable communities but in the time factor involved in any consideration of relative stability of vegetation. Selleck (1960) expresses this very clearly: 'The rift (between the two schools of thought) occurs either in the assumption that, given sufficient time, climate is the over-all controlling factor of vegetation, or in the length of time considered adequate for stabilization to occur.' In other words given a sufficiently long period of time edaphic factors would be reduced to a

common level by the action of climate and the vegetation as a whole would develop uniformity accordingly.

It is impossible to define stability without reference to a time scale and since these are usually related to the life span of man himself, vegetational changes which occur over a 'geological time scale' are not readily appreciated. If the expectation of life was one minute then a population of groundsel (*Senecio vulgaris*) would be a climax vegetation. Conversely if our life expectation was measured in thousands of years the coniferous forest subclimax of North America would be merely a successional stage which precedes the establishment of deciduous forest. Such considerations are by no means as absurd as would be imagined. There is a continuous fluctuation of climate over large areas—the Pleistocene ice-age is an outstanding example—but other less marked changes have occurred in more recent times. Beschel (1961) gives data which shows that remarkable glacier fluctuations have occurred over the last 2000 years (Fig. 3.12). The evidence is taken from a variety of sources, geomorphology, historical records and dendrochronology, and shows a series of fluctuations consistent in areas as far apart as Greenland and Africa. The control of glacial activity is dependent on the over-all climate of the area and it is clear that there is a continuous variation of climate which can be very marked over a long period of time. Such climatic fluctuations will produce a successional response in apparently stable 'climax' vegetation. Cowles (1901) was well aware of this problem: 'The condition of equilibrium is never reached, and when we say that there is an approach to the mesophytic forest, we speak only roughly and approximately. As a matter of fact we have a variable approaching a variable rather than a constant.'

Whitaker (1953) attempted to circumvent the problem of time scale by proposing an approach based on the 'prevailing climax' which was related to the maximum area covered. As Selleck (1960) points out this can be criticized since a minor constituent of a forest understory for example could become the dominant species of the next generation.

One marked aspect of the theoretical climax relative to the stages of succession leading to it is the rate of change. The initial stages of succession are usually relatively rapid, the rate of change gradually decreasing until vegetational change is at a minimum and if we assume climatic and environmental stability all directional change ceases in the 'climax'. Again Cooper (1926), one of the early protagonists in this field, expressed this aspect very well: 'The climax period comes into being insensibly. Much, or even all, of a unit succession may be characterized by a gradual diminution of the rate of change. The climax itself being merely a continuation of this process, it is not possible to mark it off absolutely from the period of more active succession.' In general terms the rate of vegetational change would seem to offer a possible means by which climax vegetation could be



Glacier advance $\uparrow$ and retreat $\downarrow$ in hypothermal time, from lichenometrical, geomorphological, historical, and dendrochronological evidence.

(1) Glacier Stanley occidental, Ruwenzori, Central Africa

(2) Ghiacciaio di Gran Neiron, Gran Paradiso, Italy

(3) Grönaufener, Stubai Alps, Tyrol

West Greenland (Locations of the glaciers are indicated on Figure 1.)

(4) Tasiussaq A

(5) Tasiussaq B

(6) Ikatussaq A

(7) Ikatussaq C

(8) Tunugdliarfik A

(9) Tunugdliarfik B

(10) Tunugdliarfik C

(11) Kugssuaq A

delimited from the terminal stages of succession, but again the definition of the *relative* rates of change in the two appears to be insurmountable.

We are forced to conclude that climax vegetation is an abstract concept which is never reached in reality due to the continuous fluctuations of the climate (*directional* over periods of hundreds of years). Clearly the climate of a region has an over-all control of the vegetation. The regional development of tundra, coniferous forest, deciduous forest, etc., in a progression from the arctic towards the equator reflects this over-all control. However within each of these zones there exists a great variety of detailed modification, imposed by other factors such as geology, physiography and human activity. Such vegetation is equally stable over long periods of time and is self-perpetuating and on this basis the polyclimax theory is more sufficient than the monoclimax theory which represents an extreme abstract ideal. That the problem is relative, is inescapable and it is only possible to refer to vegetation as in an active process of successional development as compared to a state of extremely slow change, barely distinguishable from a self-perpetuating stable 'ideal'.

It is perhaps significant that the theory of climatic climax has been built up on the study of temperate vegetation and the evidence presented by Richards (1952) clearly indicates the widespread occurrence of stable vegetation types in the tropics determined by soil conditions. Thus Richards states, 'The primary forest types of Moraballi Creek, for instance, are all found under the same climate and there is no reason to consider any one of the five as less stable than the others. No process of development and no change of soil conditions is known or can be imagined which would, for example, convert the Wallaba forest on bleached sand into mixed forest on red loam or vice versa. The Mora forest, liable to flooding, shows no tendency to develop into mixed forest and the Mora soil could not conceivably develop into a mixed forest soil. It seems that all the Moraballi Creek primary types must be regarded as of equivalent status, as the Polyclimax theory demands. Each depends on a different, but equally permanent, combination of soil and topography developing under the same set of climatic conditions.' (See also Davis and Richards 1933, 1934.)

It is conceivable that climatic variation over long time scales is absent in the equatorial region, or is minimal relative to the marked glacier activity in the arctic and resultant plant successions outlined previously. No evidence is available which would demonstrate previous vegetational types

Fig. 3.12. (*opposite*) Glacier advance and retreat in metres as summarized from lichenometrical, geomorphological, historical and dendrochronological evidence. (From Beschel 1961; courtesy of Univ. Toronto Press.)

in areas of present day Primary Rain forests and it is possible that the 'abstract' climax may in fact exist in such areas where there has been a minimum of climatic disturbance. On the other hand the fluctuation of climate has only recently been studied in detail and a decision as to the likelihood of major equatorial variations will have to wait further developments in meteorology. It is well known however that raised beaches occur around several of the large African lakes reflecting (presumably) different climatic conditions in the past.

One further aspect of the climax concept with profound implication in the delimitation of 'community units' is of importance: Clements regarded an association as a complex organism [or quasi-organism, Tansley (1920)] which arose through a variety of causes and subsequently grew, matured and died. In actively changing vegetation the association which replaces a given seral stage is different whereas in climax vegetation the 'death' of an association results in the establishment of a subsequent identical association. Implicit in this concept of the association as an organic entity or 'living organism' is the concept that climax associations can be readily recognized, *defined* and *classified*. The other extreme is presented by Gleason (1917, 1926) who proposed the individualistic concept of the plant association, which basically relates the continuously variable environment to an equally continuously variable vegetation. Thus no two associations are identical and implicit here is the fact that accordingly they cannot be classified and often cannot be clearly defined. Embodied in these two concepts are the two extremes of approach to community classification in use today. This will be considered in some detail at a later stage (see Chapter 8). In addition to this aspect of the climax association as a distinct and a recognizable entity Greig-Smith (1952*b*) points out: 'This (the complex organism of Clements) implies direct interaction between individuals both of the same and of different species.' Interaction between species or individuals of the same species can be conveniently measured by means of a χ^2 -test or by an analysis of the 'pattern' of species distribution respectively (see Chapters 2 and 6). Greig-Smith investigated several sites in secondary forest ranging from areas recently disturbed (Site D) to areas disturbed many years before the investigation and only imperceptibly different from (undisturbed) primary forest (Site B). In addition an area of primary forest was sampled for comparison (Site E). The association between species is given in Tables 3.1, 3.2 and 3.3 as the numbers of observed and expected joint occurrences of pairs of species. Clearly the maximum amount of association is present in Site D (most recently disturbed) and least evidence of association occurs in Site E (primary forest). This is clear evidence that the maximum interaction between species inherent in the 'complex organismic' concept of climax vegetation is not valid at least in tropical rain forest. Greig-Smith

Table 3.1—Expected and observed numbers of joint occurrences of pairs of species in plots at site D (secondary forest). (From Greig-Smith 1952; courtesy of J. Ecol.)

<i>Rudgea freemani</i> 72	<i>Pisonia cuspidata</i> 52.56 53	73							
<i>Amaioua corymbosa</i> 58	42.34 38*	41.76 44	<i>Rudgea freemani</i> 72						
<i>Miconia prasina</i> 58	42.34 34***	41.76 39	<i>Amaioua corymbosa</i> 58	33.64 24***					
<i>Lacistema aggregatum</i> 54	39.42 48	38.88 43	<i>Miconia prasina</i> 58	31.32 26*	31.32				
<i>Alibertia acuminata</i> 42	30.66 26*	30.24 33	<i>Lacistema aggregatum</i> 54	24.36 22.68 19*	24.36 22.68 29*				
<i>Protium guianense</i> 42	30.66 32	30.24 34	<i>Alibertia acuminata</i> 42	24.36 22.68 30**	24.36 22.68 17	17.64			
<i>Coccoloba latifolia</i> 35	25.55 27	25.20 23	<i>Protium guianense</i> 42	20.30 25*	18.90 21	14.70 11	14.70 13		
<i>Vismia guianensis</i> 23	16.79 13*	16.56 16	<i>Coccoloba latifolia</i> 35	13.34 13	13.14 10	12.42 12	9.66 8	9.66 8.05	
<i>Bactris</i> sp. 20	14.60 17	14.40 17		11.60 11	11.60 11	10.80 12	8.40 7	8.40 7.00	
<i>Iseria parviflora</i> 19	13.87 14	13.68 13		11.02 10	11.02 11	10.26 6*	7.98 6	7.98 8	6.65 4
<i>Clusia minor</i> 14	— —	— —		8.12 9	8.12 8	7.56 7	5.88 5	5.88 5	
<i>Cassia fruticosa</i> 13	— —	— —		7.54 8	7.54 5	7.02 11*	5.46 5	5.46 7	
<i>Casearia spinescens</i> 13	— —	— —		7.54 8	7.54 6	7.02 10	5.46 8	5.46 7	

The number against each species is the total number of plots in which that species occurred. The numbers against each pair of species are the expected (above) and observed (below) numbers of joint occurrences.

* $P = 0.01-0.05$, ** $P = 0.001-0.01$, *** $P = <0.001$.

thus concludes that the individualistic concept of Gleason is a more satisfactory alternative in part at least. The evidence relating the pattern of distribution of the individuals of a species in an area to the 'stability' of the vegetation, suggests equally a minimum of interaction in stable vegetation. Greig-Smith (1961) examined the different pattern scales in *Amphiphila arenaria*, sampling young developing dunes, stable dunes and dune 'slacks'. His data (Fig. 3.13) show almost complete absence of pattern in the early formation of dunes (NAD 12), a maximum of pattern in the stabilizing dunes (NAD 7, 8 and 9) and only slight indications of pattern in the most stable sites examined (NAD 2, 3 and 4). The amplitude of the peaks is proportional to the intensity of the patterns. In this example the pattern varies from one consisting of patches of slightly higher density which alternate with similar patches of lower density, to sites where the patches are more aptly described as 'clumps'. Again the evidence suggests

Table 3.2—Expected and observed numbers of joint occurrences of pairs of species in plots at site B (secondary forest). From Greig-Smith 1952; courtesy of J. Ecol.)

	<i>Cordia curassavica</i> 60					
<i>Rudgea freemani</i>	30.00					
50	34					
		<i>Rudgea freemani</i> 50				
<i>Casearia spinescens</i>	27.00	22.50				
45	31	30**				
			<i>Casearia spinescens</i> 45			
<i>Bactris</i> sp. (stems)	21.00	17.50	15.75			
35	21	18	11*			
				<i>Bactris</i> sp. (stems) 35		
<i>Fagara martinicensis</i>	19.80	16.50	14.85	11.55		
33	21	15	18	10		
					<i>Fagara martinicensis</i> 33	
<i>Bactris</i> sp. (seedlings)	19.20	16.00	14.40	11.20	10.56	
32	17	14	16	12	10	
						<i>Bactris</i> sp. (seedlings) 32
<i>Acnistus arborescens</i>	18.60	15.50	13.95	10.85	10.23	9.92
31	21	15	14	13	14	10
<i>Casearia decandra</i>	18.40	7.00	6.30			
14	8	9	13***			
<i>Casearia guianensis</i>	7.80	6.50	5.85			
13	10	9	10**			

The number against each species is the total number of plots in which that species occurred. The numbers against each pair of species are the expected (above) and observed (below) numbers of joint occurrences.

* $P = 0.01-0.05$. ** $P = 0.001-0.01$. *** $P = < 0.001$.

random distribution in the final stable vegetation, that is to say no interaction between individuals of a species.

A similar set of data is given by Kershaw (1963) collected from associations of *Calamagrostis neglecta* in Central Iceland. It behaves here as a primary coloniser of open water and remains at a reduced level of performance and density while the silting up of the area continues. The recent volcanic nature of the rock in the area results in the annual deposition of vast quantities of cindery silt on the valley floors and by an inspection of the depth of water table below a stand of *Calamagrostis* it is possible to arrange a relative time scale for each stand. The deeper the water table and the more the silting, the longer the *Calamagrostis* has maintained itself in that particular site. In detail such a method of dating would be open to severe criticism but it does give an indication of the relative age of stands. Samples were taken from numerous sites. The data (Fig. 3.14) show an identical trend. There is a minimal pattern intensity in the early stages of *Calamagrostis* establishment (Fig. 3.14a) followed by an increased intensity until silt accumulation lowers the water table to about 25 cm (Fig. 3.14b and c). At about 50 cm the pattern of *Calamagrostis* though still clear is very much reduced in intensity. This trend is continued (Fig. 3.14d-g) in the series until the maximum depth of water table

Table 3.3—Expected and observed numbers of joint occurrences of pairs of species in plots at site E (primary forest). (From Greig-Smith 1952; courtesy of J. Ecol.)

<i>Rudgea freemani</i> 45	<i>Myrcia granulata</i> 59 26.55 30				
<i>Hymenaea courbaril</i> 37	21.83 25	<i>Rudgea freemani</i> 45 16.65 17			
<i>Rinorea lindemiana</i> 33	19.47 17	14.85 20*	<i>Hymenaea courbaril</i> 37 12.21 7*		
<i>Eugenia perplexans</i> 26	15.34 17	11.70 15	<i>Rinorea lindemiana</i> 33 9.62 12	8.58 10	
<i>Peltogyne porphyrocardia</i> 24	14.16 16	10.80 8	8.88 6	7.92 5	<i>Eugenia perplexans</i> 26 6.24 7
<i>Swartzia simplex</i> 20	11.80 11	9.00 8	7.40 10	6.60 3	5.20 5
<i>Calptranthes fasciculata</i> 16	9.44 8	7.20 8	5.92 3	5.28 7	
<i>Clathrotropis brachypetala</i> 16	9.44 8	7.20 6	5.92 4	5.28 3	
<i>Brownea latifolia</i> 16	9.44 7	7.20 6	5.92 6	5.28 5	
<i>Eschweilera subglandulosa</i> 15	8.85 9	6.75 9	5.55 7		
<i>Bactris</i> sp. 14	8.26 10	6.30 7	5.18 7		

The number against each species is the total number of plots in which that species occurred. The numbers against each pair of species are the expected (above) and observed (below) numbers of joint occurrences.

$$* P = 0.01-0.05.$$

underlying *Calamagrostis* is reached at about $1\frac{1}{2}$ m in the 'desert areas', after which most vegetation disappears altogether. A further collection of data was made in the area in a topographically uniform *Rhacomitrium* heath situated at about 790 m on the flat summit of a mountain. From the remoteness and past history of the region it would appear that the area had been completely undisturbed and from the evidence outlined above little pattern should have been present, apart from that produced by the morphology of the species. Again the analysis of the data (Fig. 3.15) is consistent with the concept of a minimum of pattern (interaction between individuals) in stable vegetation. The pattern detected is due to the morphology of the plant and is equivalent to the dimensions of the area covered by the rhizome system of an individual plant.

The evidence is consistent and clear cut; it is drawn from a variety of habitats ranging from sub-arctic moss-heath to tropical forest and indicates that the original thesis of Greig-Smith's should at least be a basis for further work.

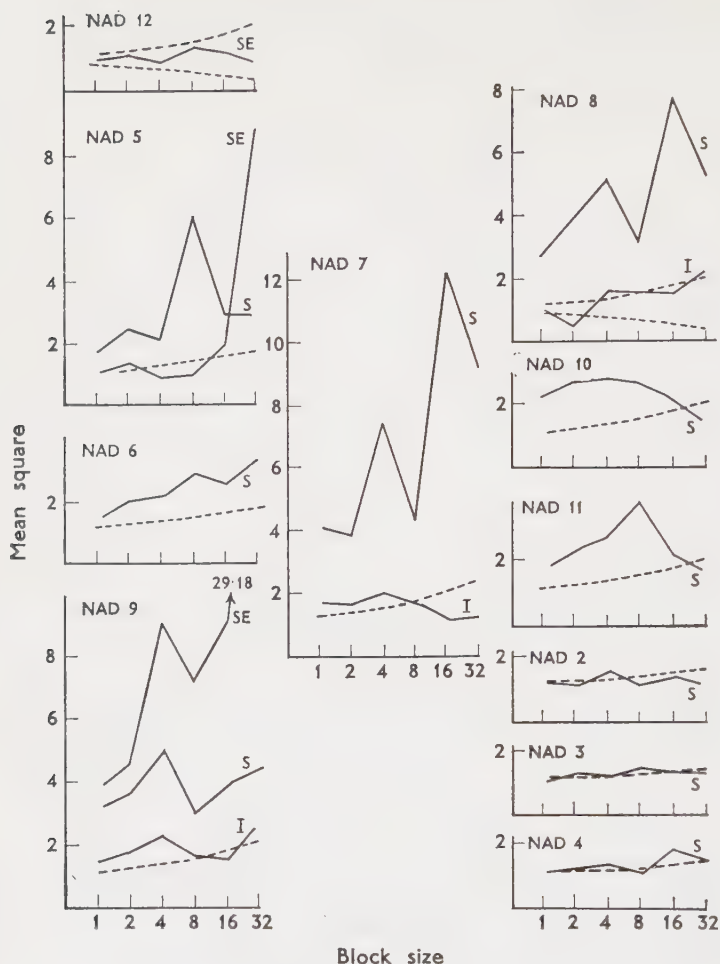


Fig. 3.13. The changing intensities of pattern of *Ammophila arenaria* in relation to dune age and stability. The dotted lines represent upper and lower 95 per cent limits for random distribution. (From Greig-Smith 1961; courtesy of *J. Ecol.*)

Conclusions

The controversy centred on the climax concept has been continuous for almost 50 years, the literature is bulky and has been condensed here to a considerable extent. It may help to clarify the position by summarizing the more important aspects:

1. Succession is defined as a directional vegetational change induced by an environmental change or by intrinsic properties of the plants.

2. The initial rate of vegetational change is high and subsequently falls to a low level after which further development is governed by very slow changes of climate or physiography. This relatively stable state is referred to as the climax.

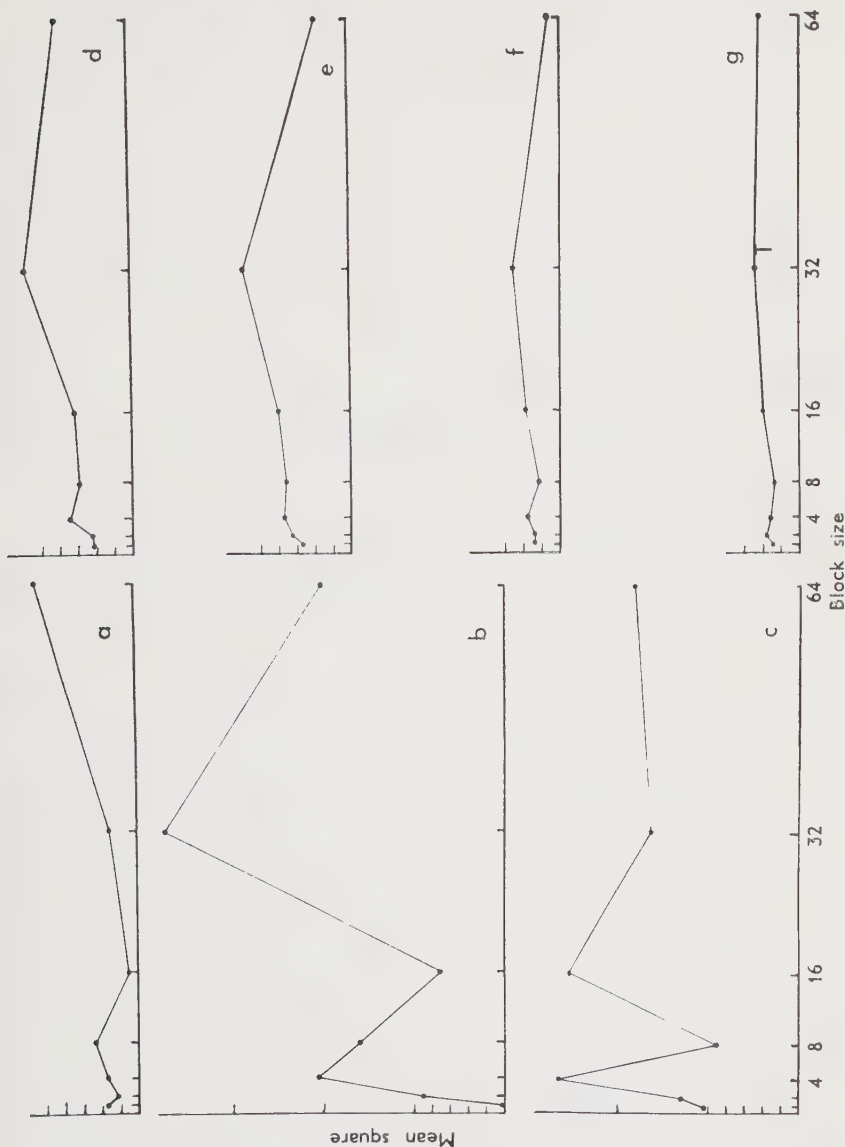


Fig. 3.14. The changing intensities of pattern of *Calamagrostis neglecta* in relation to age and stability. (From Kershaw 1963; courtesy of *Ecology*.)

3. The original 'climatic climax' is an abstract concept since climate is *not* stable and furthermore other environmental factors influence the final vegetation of an area in addition to climate. Thus the polyclimax theory is a more realistic concept.

4. Climax vegetation is defined approximately as a self-perpetuating association of plants having a maximum of stability; any change occurring is very slow, and only appreciable over extensive time scales (relative to the time scale of establishment of the climax through succession).

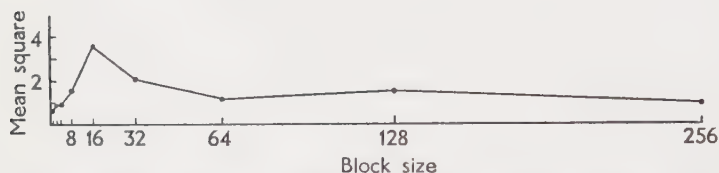


Fig. 3.15. General absence of pattern on *Carex bigelowii* growing in stable *Rhacomitrium* heath other than small scale morphological pattern (see text).
(From Kershaw 1963; courtesy of *Ecology*.)

5. Evidence shows stable vegetation to have a minimum of association between species and individuals (pattern). Thus Gleason's individualistic concept of the climax is a more satisfactory hypothesis than the 'complex organism' as envisaged by Clements.

4

Cyclic Vegetational Change

It is commonplace to regard vegetation which is stable and in equilibrium with its environment as a static entity, which having gone through various stages of succession has finally reached an ultimate level of stability and ceases to change any further. This superficial impression is misleading since in addition to the external environmental factors which regulate the over-all composition of the vegetation, there exists a series of intrinsic factors which continue to induce vegetational change. This intrinsic vegetational change is not manifested as a continuation of succession but as a cycle of events at any particular point in a community. These events are replicated many times over the whole of the community, and are apparent as a series of phases present at a number of points at any instant in time. The over-all summation of these phases constitutes the composition of the community. Thus while plant succession is a *directional change*, cyclic changes represent *fluctuations about a mean value*.

HUMMOCK AND HOLLOW CYCLE

Watt (1947a) outlined a number of examples of cyclic fluctuations containing several marked phases which are now regarded as classic examples of cyclic change. The regeneration complex which occurs on actively growing raised bog (the 'hummock and hollow cycle' as it is often called) is an outstanding example of a series of dynamic phases which are related to each other in time. The phases form a mosaic of patches, each at a different stage from its neighbours. Oswald (1923) and Godwin and Conway (1939) have shown the relation of the phases to each other by examination of the stratigraphy of the underlying peat. The initial phase is represented by *Sphagnum cuspidatum* which invades small pools of water. This species is invaded by *S. pulchrum* which in turn is replaced by *S. papillosum*. The latter species build up low hummocks which are eventually colonized by *Calluna vulgaris*, *Erica tetralix*, *Eriophorum vaginatum* and *Trichophorum caespitosum*. At a later stage the lichen species *Cladonia arbuscula* (*C. sylvatica*) enters the sequence, each sequence being abundantly preserved as stratified deposits of peat. At this stage the

sequence is identical to a 'micro-succession' and each of the subsequent stages is dependent on the reactions on the environment by its predecessors. However, as the *Calluna* ages and dies the hummock is eroded and a pool of open water re-established largely by the activity of the adjacent phases building up hummocks. Thus, under these conditions, an area of raised bog is a mosaic of patches each of which represents a phase of a cycle; each patch will progress eventually and repeatedly through the same cycle of events and although a given (small) area will change over a period of time the whole community remains essentially the same.

A similar example is drawn by Watt from grassland, where the vegetational variation is related to microtopography. Four phases are present, descriptively termed 'hollow', 'building', 'mature' and 'degenerate' (Watt 1940). The hollows are invaded by seedlings of *Festuca ovina* around which accumulates a variety of wind-borne particles in addition to humus remains of the parent plant. Over a period of time a small hummock is formed, representing the 'building' phase (Fig. 4.1). In the mature phase

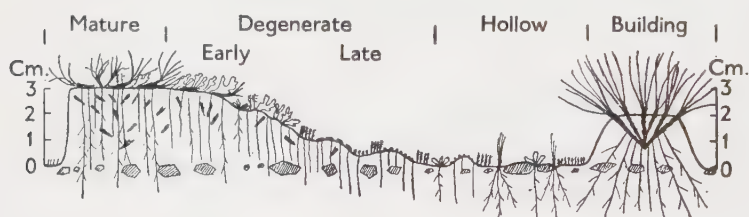


Fig. 4.1. Diagrammatic representation of the *Festuca ovina* erosion cycle indicating 'fossil' shoot bases in the soil. (From Watt 1947; courtesy of *J. Ecol.*)

the hummocks reach a height of about 4 cm and are colonized by several lichen species notably *Cladonia alpicornis* and *C. rangiformis*. The lichen species slowly assume a more dominant role in the early stages of the 'degenerate' phase and are gradually replaced by crustaceous lichen species. Erosion of the hummock follows completing the fully cycle of events back to the 'hollow' phase. Again the over-all structure and composition of the community remains unchanged since each phase is represented by a mosaic of cyclic units related spatially to each other as well as representing a time sequence.

The occurrence of cyclical phases is not restricted to perennial herbaceous species and Watt (1947) also describes a cyclical development which occurs over a long period in beech woodland on chalk plateau. Following the death of a full grown tree the gap that is left is initially devoid of vegetation and represents the first phase of the cycle. This is invaded initially by *Oxalis* and subsequently by *Rubus*, representing the next

two phases of the cycle. Concurrently beech and ash seedlings become established forming a 'reproduction circle' (Watt 1925) with the ash in the centre surrounded by a circle of young beech originating from seed shed by the surrounding mature beech. Eventually the ash is over-topped by the beech saplings and the gap finally closed. The cycle is finally completed by the ultimate degeneration and death of the beech colonizers initiating the same cycle again. The time scale in this example is very long but the nature of the process is identical.

In general the sequence of events is similar in all the examples given by Watt (1947a) and these he descriptively terms pioneer, building, mature

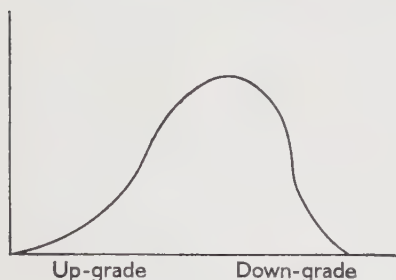


Fig. 4.2. Generalized productivity curve. (Redrawn from Watt 1947.)

and degenerate. The productivity of each phase appears to follow a generalized curve of increasing productivity in the early phases of a cycle, leading to an optimum in the mature phase, and followed by reduced productivity in the degenerate phase (Fig. 4.2). Billings and Mooney (1959) give an account of an extremely interesting cycle in tundra vegetation at 11,000 ft in the Medicine Bow Mountains of

southern Wyoming. The area as a whole is subjected to intense soil frost action and the valley bottom is covered with actively forming frost hummocks of peat and stone polygons. The occurrence of frost hummocks and polygons is extremely characteristic of arctic and sub-arctic zones, where intense frost produces a number of marked topographical features. Billings and Mooney relate the formation of polygons in this area to the degradation of the frost hummocks of peat. When a hummock rises to a certain level so that it protrudes above the general level of the snow in winter, the species on the crest of the hummock are killed and eroded away by the repeated action of wind and wind-borne ice/snow particles. With continued exposure the hummock itself is eroded exposing rocks and silt which are pushed up concurrently from below by further frost action. Eventually the hummock is completely eroded to its base and this stage appears as a stone polygon surrounded with a 'rim' of peat.

The water table in the whole area fluctuates from year to year; the hollows usually are fairly wet and often whole areas of polygons are completely submerged. During these submerged periods the hummock formation appears to be initiated by *Carex aquatilis* which invades the rocky intervals of the polygons. The general sequence of events is shown in Fig. 4.3 below. Following the establishment of *C. aquatilis*, *Sedum*

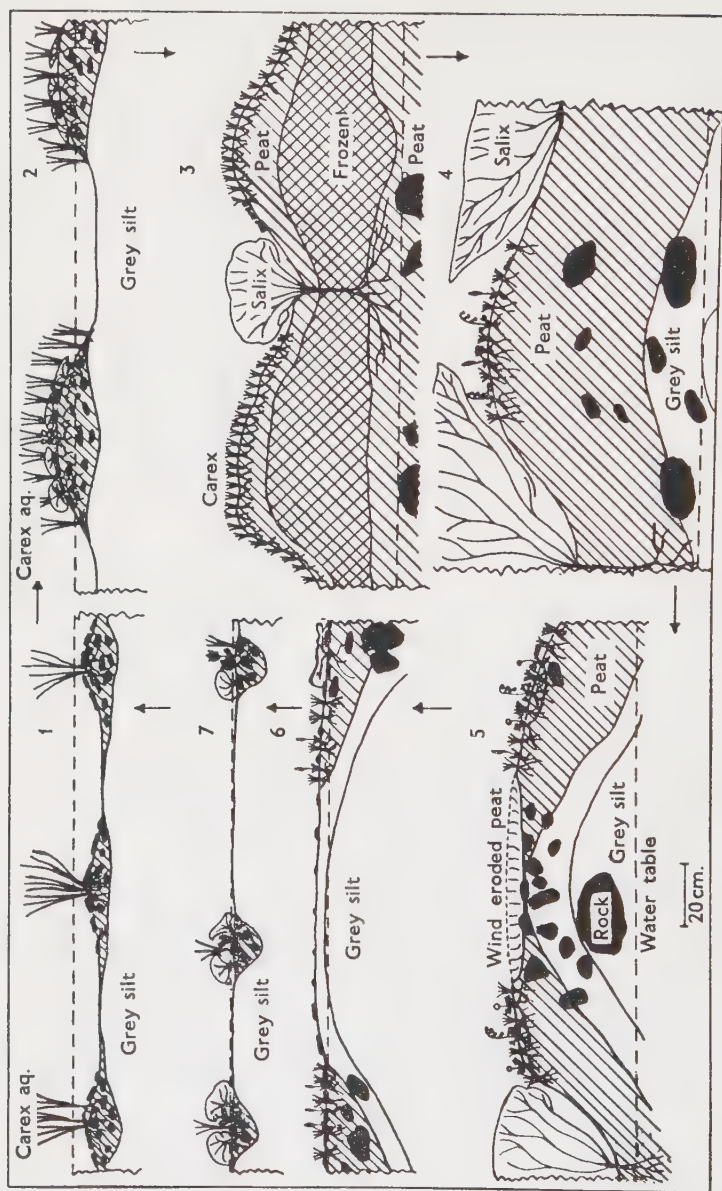


Fig. 4.3. Diagrammatic representation of the hummock, frost scar and polygon cycle. (From Billings and Mark 1961; courtesy of *Ecology*.)

rhodanthum and several bryophyte species become established. Eventually these species are replaced by *Geum turbinatum* and *Polygonum viviparum* which form a closed turf with other additional species on the mature hummocks. The erosion commences at this stage of the cycle and subsequent drowning of polygons initiates the next cycle. Thus there is a continuous cycle of change, hummocks alternating with the centre of polygons and the margin of the polygons alternating with subsequent hummocks. The general phasic development of this cycle is strikingly similar to the hummock and hollow cycles discussed by Watt (1947). The mechanism is partly different and the species involved obviously different, but the same general principle is common to all three cases. The pioneer phase in this instance is dominated by *Carex aquatilis*, the building phase by *Carex* and *Sedum* and the mature phase by *Geum* and *Polygonum*.

MARGINAL EFFECTS

Cyclic phases as described above are partly dependent on intrinsic properties of the plants themselves and partly dependent on intrinsic properties of the community both of which are modified and controlled to a greater or lesser extent by the environment. Thus the ability of *Sphagnum papillosum* to form hummocks is an intrinsic property of that species, the availability of the other species involved in the cycle is an intrinsic property of the community, and the final partial erosion of the hummock is a result of environmental control. The downgrade phases of the cycle are terminated by erosion of the hummock but it is interesting to speculate as to the actual initiation of the downgrade phase. A possible explanation lies in the relationship between the general vigour of a perennial plant and its age. This important concept was originally outlined by Watt (1947*b*) in relation to the vigour of bracken invading grassland where the marginal zone was considerably taller and apparently more vigorous than in the 'hinterland'. The difference in height of the fronds in the margin and hinterland is considerable (Fig. 4.4). The immediate possibility which would account for this 'marginal effect' would be the presence of some factor necessary for the full development of the fronds which is markedly reduced in quantity by the advancing front and is in short supply in the hinterland. However, analysis of the soil (Table 4.1) shows no consistent trend to support such a hypothesis and furthermore the addition of different combinations of fertilizers containing nitrogen, potash and phosphorus to sample plots in the hinterland had no significant effect.

The significant feature is the progressive increase of rhizome age back from the margin to the hinterland where the oldest part of the rhizome decays and lateral shoots become separated as individuals. Thus the margin has a large number of young even-aged rhizomes orientated parallel to

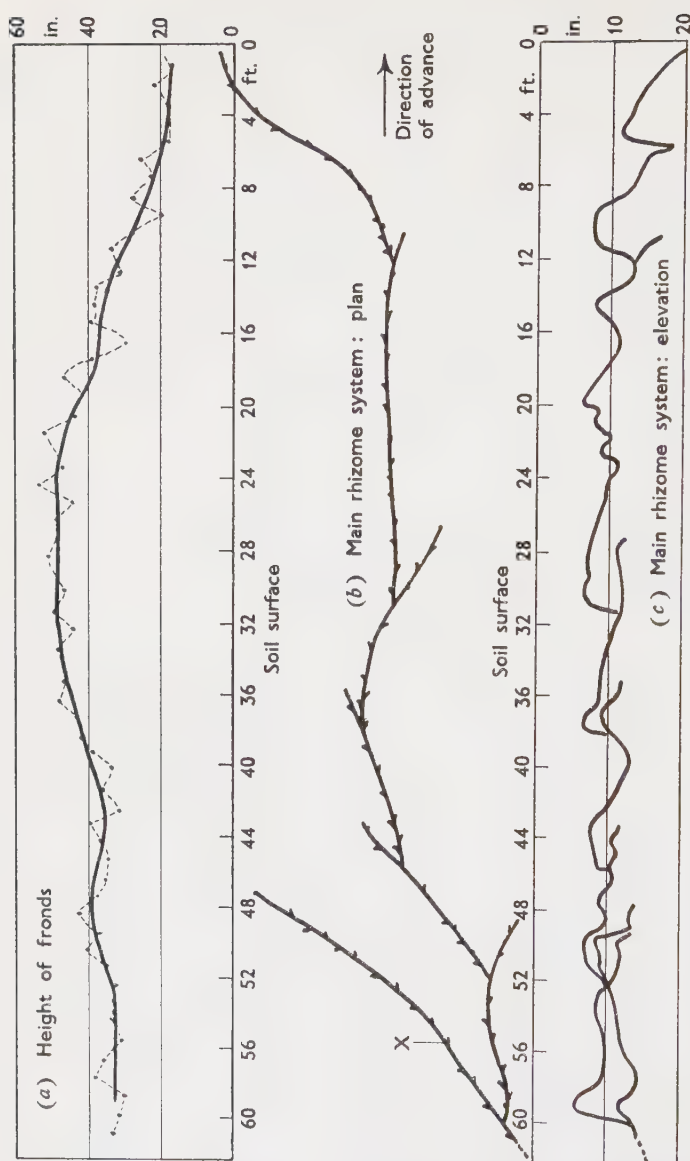


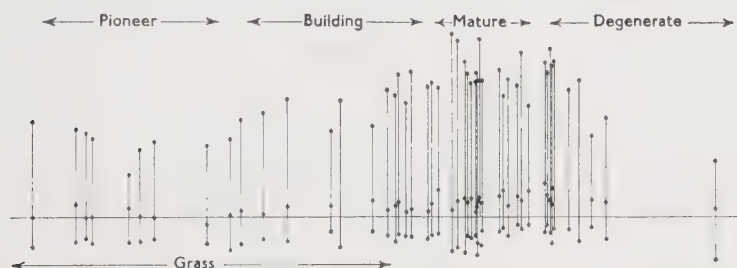
Fig. 4.4. (a) the average height of fronds across the advancing margin of bracken; (b) plan and (c) elevation of main rhizome. (From Watt 1940; courtesy of *New Phytol.*)

each other. These younger parts of the rhizome produce larger and more vigorous shoots resulting in the marked marginal effect. Conversely in the hinterland the rhizomes are initially much older and the shoots smaller. As the main rhizome decays lateral shoots of different ages are separated as individuals each of which will subsequently follow the same progressive change of vigour as each individual ages. Thus the hinterland consists of

Table 4.1—Soil data from surface layers (0–7.6 cm) in different zones of bracken invading grassland. (From Watt 1940; courtesy of *New Phytol.*)

	In grassland	In zone of maximum height	In dense uniform bracken	In hinterland
pH	4.2	4.0	3.8	4.0
Carbon per cent	1.785	1.425	1.740	1.610
Carbon/Nitrogen	19.40	19.79	19.12	19.63
Exchangeable Calcium in marginal effect	1.44	1.28	1.28	1.36
Total exchangeable bases	2.40	2.00	1.61	1.61

very unevenly aged groups of individuals at all stages of the cycle forming a mosaic of phases. In addition to the height of frond being at its maximum in the mature phase the length of petiole above ground follows the same trend and the length of petiole below ground level follows an inverse trend (Fig. 4.5). There is a marked relationship between the age of the

**Fig. 4.5.** The positions and dimensions of bracken fronds showing the sequence of phases from pioneer to degenerate. The dots indicate the depth of origin, petiole length and height of fronds. (From Watt 1947; courtesy of *New Phytol.*)

rhizome and its morphology, and also between the vigour or performance of the aerial shoots from young and older parts of the same rhizome. This feature may explain the onset of the downgrade stage of the cyclic phases outlined above. As the principal species of the mature phase age, their performance falls markedly and the degenerate phase commences.

The general occurrence of a phasic development of perennial plants is indicated from the numerous reports of marginal effects in the literature. Kershaw (1962a) describes a very marked marginal effect in *Eriophorum angustifolium* invading a *Salix herbacea*/*Polygonum viviparum* community

in central Iceland. The density and performance (expressed as leaf length, leaf width and length of leaf tip) both show a similar relationship to the advancing front in *Pteridium* described by Watt (Figs. 4.6, 4.7 and 4.8).

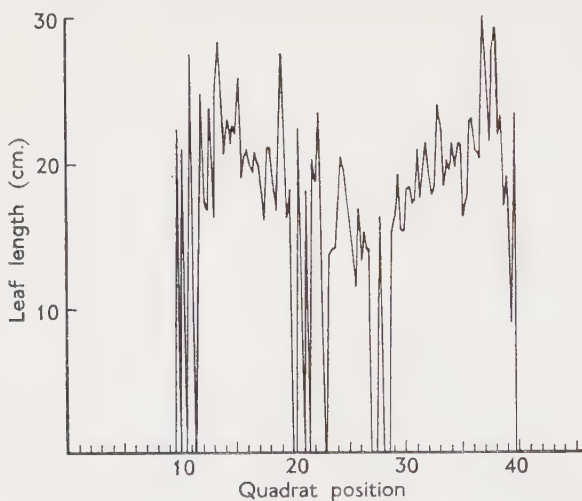


Fig. 4.6. The variation of performance of *Eriophorum* (leaf length) along a transect running through the circular advancing margin. (From Kershaw 1962; courtesy of *J. Ecol.*)

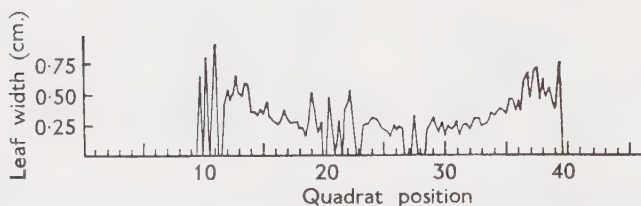


Fig. 4.7. The variation of performance of *Eriophorum* (leaf width) along a transect running through the circular advancing margin. (From Kershaw 1962; courtesy of *J. Ecol.*)

Similarly Ovington (1953), Caldwell (1957) and Penzes (1958, 1960) have described numerous examples of advancing fronts of even-aged rhizomes at an optimum level of performance relative to the hinterland with its very much lower level. Watt (1955) shows that *Calluna* follows the same phase development and furthermore where *Pteridium* is present there is an inverse relationship between the two species. Where *Calluna* is at its building/mature phase, competing bracken is at its minimum development. Similarly where *Calluna* is in its degenerate phase, bracken is at the

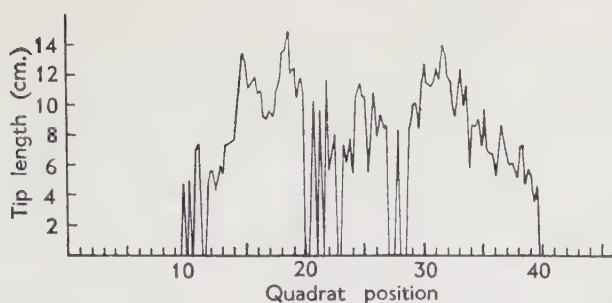


Fig. 4.8. The variation of performance of *Eriophorum* (tip length) along a transect running through the circular advancing margin. The length of tip is inversely proportional to performance. (From Kershaw 1962; courtesy of *J. Ecol.*)

building or mature phase. Thus concurrently the competitive ability changes with the phasic series pioneer, building, mature and degenerate. The phasic development of *Pteridium* and *Calluna* have been confirmed by Anderson (1961*a*, 1961*b*) and Nicholson and Robertson (1958).

INTERACTION OF AGE AND PERFORMANCE

Confirmation of the relationship between age of an individual and its competitive ability is given by Kershaw (1962). The effect of the advancing front of *Eriophorum* (see p. 70) was related to the density of *Salix herbacea*, the density of *Salix* being inversely related to the density and performance of *Eriophorum* (Figs. 4.9 and 4.10). In effect where the density of *Salix* was at a minimum *Eriophorum* had a maximum level of performance and abundance, indicating the greater competitive ability of

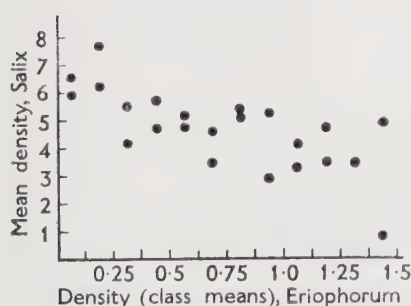


Fig. 4.9. Relationship between the densities of *Eriophorum* and *Salix herbacea* (see text). (From Kershaw 1962; courtesy of *J. Ecol.*)

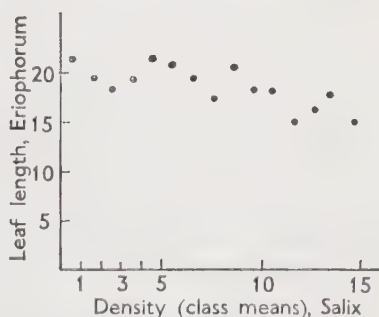


Fig. 4.10. Relationship between the density of *Salix herbacea* and performance (leaf length) of *Eriophorum* (see text). (From Kershaw 1962; courtesy of *J. Ecol.*)

Eriophorum in its building and mature phases. Thus in general terms there exists a direct relationship between age, performance and competitive ability, potentially, for most if not all perennial plants.

The quantitative assessment of the age/performance relation presents some difficulties since it is often impossible to determine the age of most herbaceous perennials. Data for two species only are available (Kershaw 1960b, 1962c), for *Alchemilla alpina* and *Carex bigelowii* the assessment of age being based on ring counts and the rhizome morphology respectively. The mean leaf diameter and leaf number per individual of *Alchemilla* were used as a measure of performance, each individual being aged by a count of growth rings. A considerable variation of performance is present (Fig. 4.11) between individuals of the same age reflecting local environ-

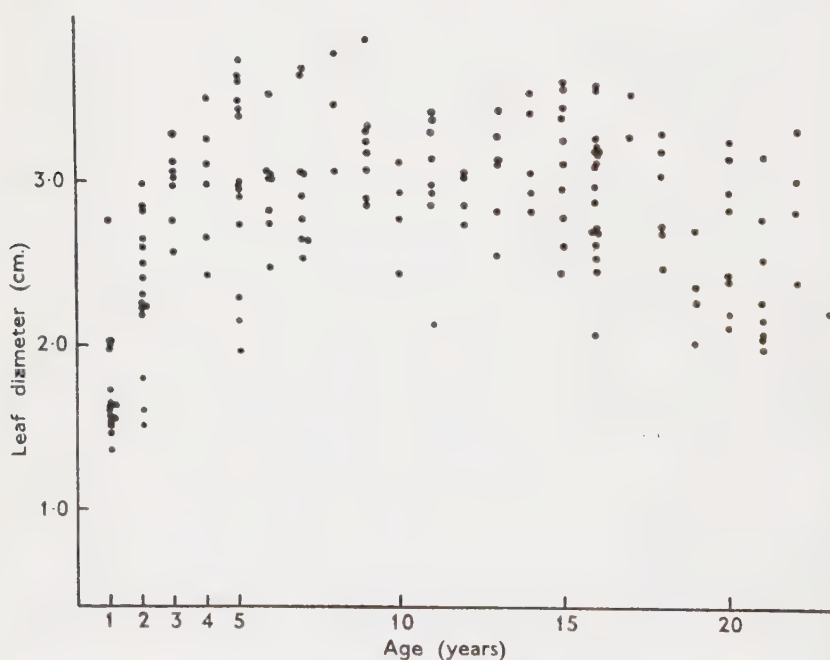


Fig. 4.11. The scatter of mean values of leaf diameter (performance) for individual plants of *Alchemilla alpina* of all ages. (From Kershaw 1960; courtesy of *J. Ecol.*)

mental effects, but the total data shows a clear rise and fall in the relationship between performance and age. A regression of the form $Y = a + bx + cx^2$ is highly significant and indicates the mature phase to fall within the age groups 9–15 years (Fig. 4.12). The relationship between leaf number and age is similar but with a larger scatter of values (Fig. 4.13). The data

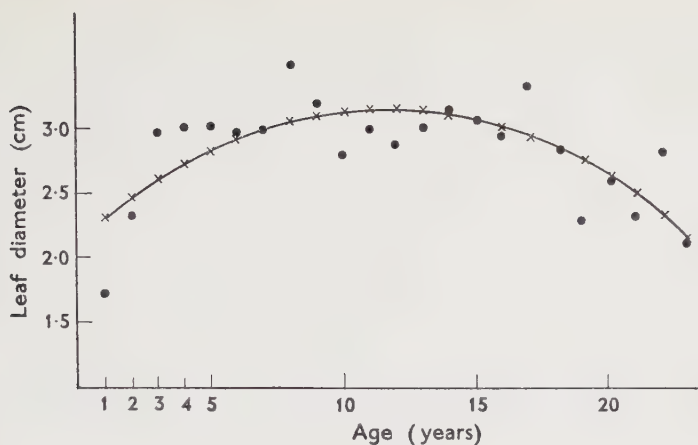


Fig. 4.12. Fitted curve of the type $Y = a + bx + cx^2$ for the total leaf diameter/age data of *Alchemilla*. (From Kershaw 1960; courtesy of J. Ecol.)

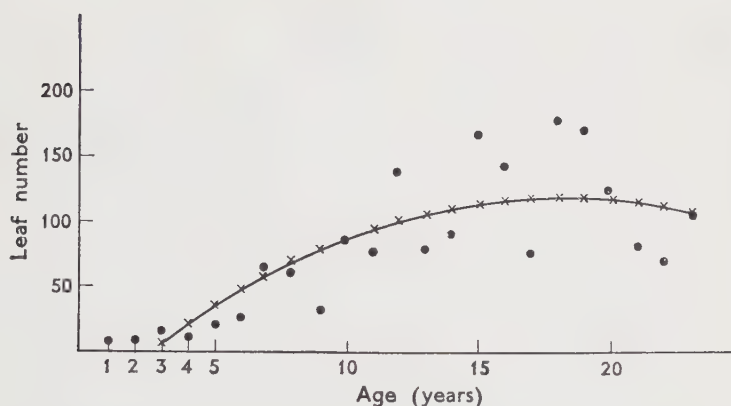


Fig. 4.13. Fitted curve of the type $Y = a + bx + cx^2$ for the total number of leaves/age data of *Alchemilla*. (From Kershaw 1960; courtesy of J. Ecol.)

clearly confirm the relationship initially proposed by Watt to describe the phasic development of *Pteridium*. The data for *Carex bigelowii* is similar (Fig. 4.14). Leaf length and leaf width are used as a measure of the performance and the age of a rhizome system determined by careful morphological examination. At the end of a season's growth, the aerial parts die, the basal leaf sheaths remain as a humified 'knot' on the rhizome and it is relatively straightforward to determine the age of a rhizome system with a fair degree of accuracy.

6—Q.D.E.

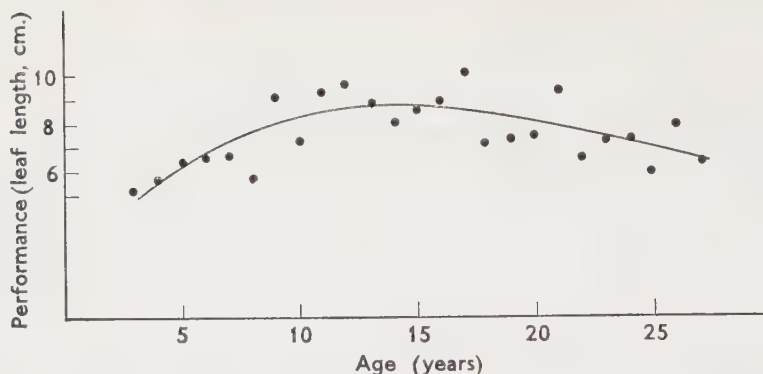


Fig. 4.14. Performance/age relationship of *Carex bigelowii* as expressed by leaf length. A curve of the type $Y = a + bx + cx^2$ is fitted. (From Kershaw 1962; courtesy of J. Ecol.)

It seems highly probable that similar growth curves will exist for many other perennial species. For this reason phasic development and relationships between other species are likely to be widespread and the lack of additional evidence reflects the difficulties of detecting such cyclic relationships. Phasic development involving several species in a definite sequence seems unlikely to be as widespread as a mosaic of density phases reflecting the age/performance interaction with the attendant variation of competitive ability and the potential effects on associated species. Thus a stable community will be in a constant state of phasic fluctuation one species becoming locally more abundant as another species reaches its degenerate phase, the fluctuation in density being however slight and not visually distinct. Only by careful quantitative measurement of abundance and performance can phasic developments be detected in vegetation where there is a complete cover, and then only in those species which possess some morphological or anatomical feature which enables their age to be assessed. Where the vegetational cover is discontinuous, and the degenerate stage is eroded and followed by a 'bare' phase, cyclic relationships become visually more obvious but apparently rather uncommon. However, it is clear that this form of relationship is likely to be widespread and is the mechanism underlying the dynamic nature of vegetation. The initial demonstration of non-randomness in vegetation was somewhat surprising to the early workers in this field and they were at a loss to account for it apart from consideration of morphology and localized seed dispersal (see Chapter 7, p. 114). In the light of the evidence outlined above it is clear that a non-random distribution of individuals will always occur however uniform the environment, as long as several age groups are present.

Such patterns have been detected by Kershaw (1958, 1962) in *Agrostis*

tenuis, *Calamagrostis neglecta* and *Carex bigelowii* where small clumps of tillers a few centimetres in diameter are formed from different rhizome systems (p. 126). A typical turf from upland rough grazing in Wales consisted of a mosaic of *Agrostis* tillers surrounded by *Festuca* and various bryophyte species, and in all cases the groups of *Agrostis* shoots arose from several different rhizome systems (Figs. 7.8 and 7.9). The mechanism of this rhizome orientation is somewhat obscure but if any one group of tillers is considered in isolation over a period of time it follows a typical phasic development. Initially a group of young tillers is established from a few pioneer rhizomes, representing the pioneer stage. The following year the clump produces several axillary shoots and is enlarged by the arrival of further pioneer rhizomes; the building phase. In subsequent years this process is continued through a mature phase until there is a preponderance of dead tiller bases in the clump and the degenerate phase follows with increasing numbers of dead tiller bases and weaker aerial shoots. Finally the whole phase is represented merely by humified remains of shoot bases which can be found underlying a small patch of *Festuca*. By careful examination the different phases can be picked out by the size and colour of the leaves of *Agrostis*. The early phases have bright green small leaves, the building phase bright green and larger leaves with little evidence of dead leaf bases. The mature phase though similar has a number of dead leaf bases present, a trend which becomes increasingly evident in the degenerate phase where there is a preponderance of dead leaves with a few small and often yellowish-green aerial leaves.

The underlying mechanism of these varying levels of performance of individual plants and the corresponding relationship of their competitive ability has been obscure. Recently however a fuller understanding of the competition for light by crop plants has been achieved (Donald 1961) and these results seem to be of direct significance in this present context. If water and nutrients are in adequate supply, then light will become the limiting factor controlling rate of growth and the production of dry matter. In any stratified vegetation there exists a very sharp decline in light intensity from the surface layers downwards and very often the lowest leaves will make a negative contribution to the net assimilation of the whole 'canopy' since the light intensity will be insufficient to keep them above compensation point. The respiration of these lower leaves in fact exceeds their photosynthesis. Expressing leaf area as a leaf area index (i.e. leaf area per unit of land area), it can be shown theoretically that if the relationship of photosynthesis to respiration is extrapolated for a continued increase of leaf area index, then a leaf area index will be reached at which the respiration of the whole canopy of foliage will equal its photosynthesis. Under natural conditions there is little evidence to suggest that this state is ever achieved in crop plants, but it seems more likely that perennial

plants may reach this compensation point. From an ecological point of view it is this possibility which is of significance, since not only are the aerial parts of importance but the underground parts also. Thus a perennial plant with an extensive rhizome system has a large actively respiring volume with a relatively small (theoretically peripheral) zone of aerial shoots, and the compensation point is likely to be reached or exceeded in old individuals. *Carex bigelowii* is a case in point. A complete rhizome system 20 years of age will cover one square metre with a complex system of branches, each ultimate branch having a terminal aerial shoot and only one or two axillary shoots in the last two years' growth increment. In such a system it is very likely that the compensation point has been reached or exceeded and the plant is in its 'degenerate phase'. Conversely a young plant of 6–12 years of age has a much less extensive rhizome system and with a normally developed 'leaf canopy' is at its optimum level of growth.

Went (1957) has referred to the build-up of non-photosynthesizing tissues in old strawberry plants until the whole plant is barely at compensation point at a high light intensity and it seems probable that the ratio between the photosynthesis and respiration of a perennial plant largely controls its general level of performance and its ability to compete with its neighbours. This possible explanation is equally satisfactory when applied to the parts of a fragmented degenerate individual. In *Alchemilla*, *Agrostis*, *Pteridium* and *Carex* the older parts of the rhizome slowly decay and as the zone of decay reaches a lateral branch this becomes separated off as an individual. The oldest plants of low performance thus release 'propagules' with, initially at least, a low performance but with a morphologically optimal age. A propagule from a 25-year-old parent is likely to be 8–12 years of age. However the average performance of all individuals in this age group is optimal and accordingly it would appear that the level of performance of such a propagule immediately rises to its 'morphological age'. This seems quite logical when considered as a small rhizome system being severed from a very large system which was respiring actively. Immediately the photosynthesis/respiration ratio becomes unequal, the terminal leaves provide an excess of metabolites relative to the now small rhizome system, and active growth can take place at once.

5 Correlation and the Causal Factors of Positive and Negative Association between Species

CORRELATION COEFFICIENTS

THE detection of association by means of a contingency table and calculation of χ^2 , implies a proportion of quadrats which do not contain the species under consideration. An important aspect of community structure is the relationship between the *quantities* of species present, rather than the mere presence or absence of the species. Two species in fact may show a marked negative *correlation*, the amount of one species varying inversely with that of the other even in cases when all the quadrats of the sample contain at least one individual of each species, and hence cannot be analysed by the χ^2 method. Where the data are in the form of cover, frequency or density, a correlation coefficient is the simplest measure which detects any possible relationship between them. Similarly relationships between abundance of a species and measurements of the environment can be detected by correlation coefficients. A similar approach is to calculate the equation which best fits the data, or in other words to calculate the 'regression' of one factor y on another x . Regression analysis is of considerable use in many ecological investigations, but details of the method are beyond the scope of this book and the student may refer to any elementary textbook of statistics. In general a regression analysis is more informative than a correlation coefficient which merely gives information on the level of the relationship. Furthermore if the independent variate x is not normally distributed, the use of the correlation coefficient is, strictly speaking, not valid. It should also be noted that the relationship may in fact not be a linear one and accordingly a correlation coefficient may not reach a significant level. In such a case the calculation of a curved regression (quadratic or high power regression) would be a possible approach.

However, despite these shortcomings, correlation is still of considerable use in ecology. The use and calculation of a correlation coefficient can be suitably demonstrated with the data which have been given in the form of a histogram previously (Fig. 2.6). These illustrate the floristic change

along a transect running from a zone of vegetation on clay with flints down into chalk grassland on the North Downs. The actual data are given below in Table 5.1. From a scatter diagram (Fig. 2.4) a clear impression is given of the general negative relationship between the percentage covers of *Agrostis* and *Festuca*.

Table 5.1—(see text)

<i>Agrostis tenuis</i> cover values	
x_1	7 11 11 3 23 7 11 10 7 13 21 13 18 8 1
	12 9 4 3 3 6 1 9 8 5 4 4 3 8 6
	7 5 15 13 21 42 36 40 31 34 19 37 35 47 20
	31 36 13 16 22 46 35 31 18 9 27 19 16 22 19
	12 21 7 10 9 9 8 - 10 5 - 7 33 9 3 19 15
	11 10 25 27 15 7 6 8 14 8 22 17 4 23 7 10 11
	23 19 7 7 30 23 16 19 39 35 23 26 32 26 20 21 34
	36 27 20 26 29 28 45 43 28 38 25 56 41 28 33 26 37
<i>Festuca rubra</i> Cover values	
x_2	22 22 33 37 24 22 1 30 19 22 21 19 17 32 43
	22 38 25 20 18 34 43 27 13 30 27 15 13 22 15
	31 22 15 14 17 10 7 10 24 7 11 4 6 8 8
	7 14 27 19 14 5 13 12 27 25 16 8 13 18 -
	12 25 26 25 18 16 23 28 32 29 31 28 13 42 28 20 28
	15 19 20 8 25 19 27 17 16 22 26 18 23 13 6 14 23
	29 13 24 7 2 24 24 21 9 10 20 8 4 12 24 10 6
	1 5 1 2 - 7 11 8 12 2 2 1 4 5 - 2 -

The correlation coefficient is calculated as follows:

$$n = 128$$

$$Sx_1 = 2,379, \quad Sx_1^2 = 63,803, \quad \frac{(Sx_1)^2}{n} = 44,216$$

$$S(x_1 - \bar{x}_1)^2 = Sx_1^2 - \frac{(Sx_1)^2}{n}$$

$$= 63,803 - 44,216 = 19,587$$

$$Sx_2 = 2,196, \quad Sx_2^2 = 51,246, \quad \frac{(Sx_2)^2}{n} = 37,675$$

$$S(x_2 - \bar{x}_2)^2 = Sx_2^2 - \frac{(Sx_2)^2}{n}$$

$$= 51,246 - 37,675 = 13,571$$

$$S(x_1 \cdot x_2) = 29,939, \quad \frac{Sx_1 \cdot Sx_2}{n} = 40,815$$

$$S[(x_1 - \bar{x}_1) \cdot (x_2 - \bar{x}_2)] = Sx_1x_2 - \frac{Sx_1Sx_2}{n}$$

$$= 29,939 - 40,815 = -10,876$$

Correlation coefficient

$$r = \frac{S[x_1 - \bar{x}_1](x_2 - \bar{x}_2)}{\sqrt{[S(x_1 - \bar{x}_1)^2 \cdot S(x_2 - \bar{x}_2)^2]}} = \frac{-10,876}{16,304} = -0.667$$

The number of pairs of observations is 128 and accordingly the table of r -values is entered with 126 degrees of freedom (for table of r -values see Fisher and Yates 1958). For 100 degrees of freedom the probability of exceeding an r -value of 0.3211 by chance is 0.001, i.e. the negative correlation between *Festuca* and *Agrostis* is a highly significant one.

This result is not unexpected and the correlation between the two species is in fact readily appreciated from the scatter diagram (Fig. 2.4). It is often worthwhile to plot a scatter diagram before attempting to calculate a correlation coefficient, since those cases which are clearly not related in any way can be rejected without resorting to what can be a lengthy computation. Valuable information can thus be readily obtained of the level of association between pairs of species or of correlation between a species and the environmental factors, but such analyses can be undertaken only when the initial collection of data is adequately made. When designing a sampling method it is always advisable to bear in mind the possibility that there will be some degree of association or correlation between the species themselves and also with the environment, and wherever possible one should obtain the field data in a quantitative form. Where data exist that are partly (or wholly) qualitative, the analysis can present some difficulty and the resulting information is often limited. (For detailed consideration of such methods the student is referred to Greig-Smith (1957).) *It is important to realize that trends in correlation will depend on the sizes of the quadrats which are used in the sampling* and results should always be considered with this fact in mind.

CAUSALITY OF ASSOCIATION OR CORRELATION BETWEEN SPECIES

Most, if not all, data on the relative abundance of species in a given area will contain one or several correlations of species. The presence of such correlations reflects the pattern or, more usually, several scales of pattern in the vegetation. The existence of pattern in vegetation and the general factors underlying such patterns are dealt with in Chapter 6, but it is necessary to consider at this point in more detail some of the factors that are operative. These causal factors can be studied either by using the techniques available for the detection of pattern (Chapter 6), or by the use of association, correlation, or regression techniques. The two methods of analysis are very closely linked and are only treated separately here for the

sake of clarity. The causal factors are split into four sections for convenience, each section represents the level of detail at which it is studied rather than any rigid classification.

SIMILAR OR DISSIMILAR ENVIRONMENTAL REQUIREMENTS

This is probably one of the fundamental reasons for negative or positive relationships that exist between species. On a large scale and with an obvious difference of species composition in two areas such correlations between species lead to the separation of groupings which typify a 'community' (see below and Chapter 8). On a smaller scale such relationships are rarely as obvious and usually need a careful quantitative approach to detect their existence.

An example of such an environmentally controlled relationship is taken from an area of hummocky grassland associated with a calcareous mire. The data for *Carex lepidocarpa*, *C. flacca* and *Potentilla erecta* (Table 5.2) were obtained in the form of frequency, from 150 quadrats positioned by using random co-ordinates (approximately half the sample was related to a hummock). The apparent preference of *Potentilla* for the hummocks and conversely the preference of the *Carex* species for the hollows is readily tested by means of a *t*-test which shows a highly significant difference between the species. This difference is not readily visible on even a close examination of the area though an explanation in general terms is not difficult.

The 'hollows' act as runnels for base-rich water after a period of heavy rain and the pH of the soil is thus neutral to slightly alkaline. Conversely the tops of the hummocks are not affected by calcareous run-off and with leaching over a period of years, together with the steady accumulation of humus, have a pH of about 5.6–5.8 (slightly acidic).

Table 5.2—The relation between topography and the abundance of *Carex lepidocarpa*, *C. flacca* and *Potentilla erecta*

Species	Mean frequency		S.E.	Difference between frequencies	<i>t</i>	<i>p</i>
	Hummock	Hollow				
<i>Carex lepidocarpa</i>	3.15	5.34	0.4163	2.19	5.260	0.001
<i>C. flacca</i>	0.82	2.0	0.2963	1.18	3.986	0.001
<i>Potentilla erecta</i>	4.19	1.38	0.1967	2.81	14.264	0.001

It is most probable that the distribution of these species is not governed directly by the pH of the soil, but by other factors which are in turn correlated with pH. The relationship between the environment is thus most

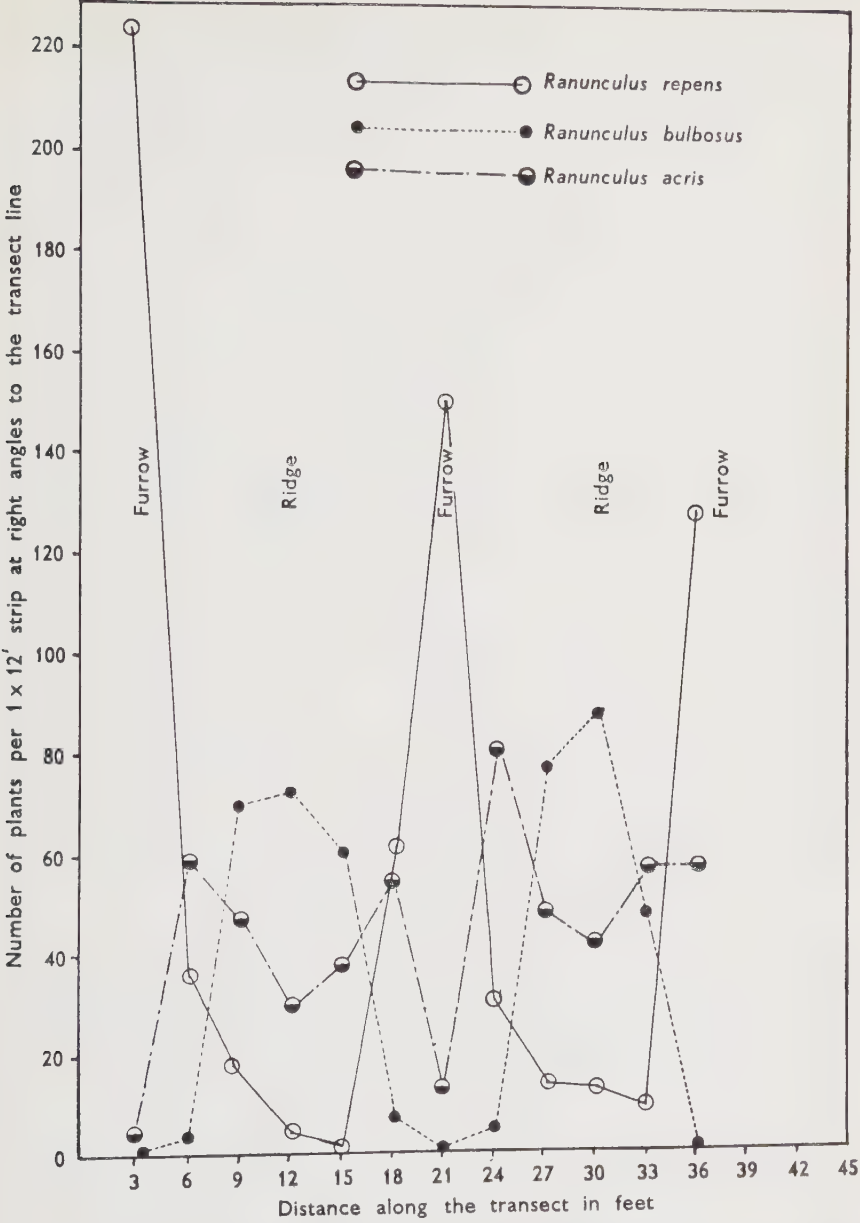


Fig. 5.1. The distribution of three species of *Ranunculus* on ridge and furrow grassland. (From Harper and Sagar 1953; courtesy of British Weed Control Council.)

easily appreciated by relating their abundance in a sample quadrat to pH.

This relationship of abundance and topography obviously leads to correlations (positive or negative) between pairs of species. In this example the distribution of the species is not sharply controlled by topography but merely influenced differentially by hummocks and hollows. The relationship accordingly cannot be appreciated merely by an inspection of the area.

Harper and Sagar (1953) have shown the spatial distribution of *Ranunculus repens*, *R. bulbosus* and *R. acris* shows a marked correlation with drainage. They investigated the relative abundance of the species along a transect orientated at right angles to furrows and ridges in a permanent pasture. The results (Fig. 5.1) show quite clearly the differential environmental requirements of the three species, *Ranunculus repens* being abundant in the furrows, *R. bulbosus* more abundant on the ridges and *R. acris* showing an intermediate distribution on the sides of the ridges. Seedling establishment under experimental conditions at three levels of drainage suggest it is this part of the life cycle, i.e. germination and early establishment, which is susceptible to the drainage of the area as a whole (Fig. 5.2).

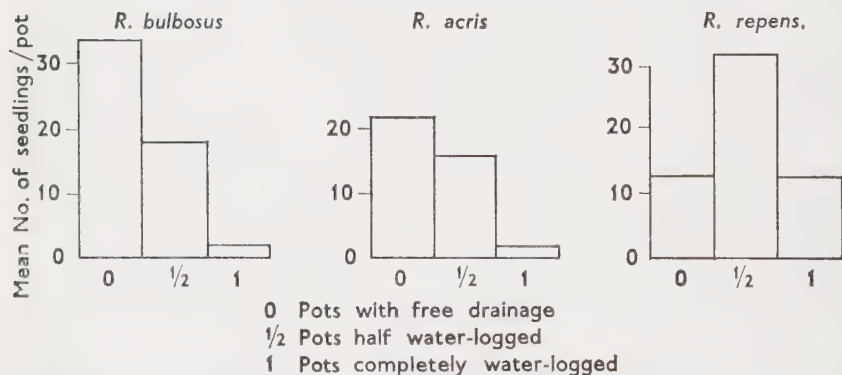


Fig. 5.2. The early establishment of three species of *Ranunculus* sown in pots with the water table maintained at different levels. Sowings were made on June 26 1953 and counts made on July 28 1953. (From Harper and Sagar 1953; courtesy of British Weed Control Council.)

These results from a markedly variable habitat can be related to the non-random distribution of *Ranunculus* in more homogeneous grassland. Micro-variation of drainage, will modify other nutritional factors to a greater or lesser extent, which will in turn influence the relative abundance of each species in a small area, and lead to negative correlation between them and to marked non-randomness in the population (see also Chapter 7, p. 114).

Both these examples are related to micro-topography and to its effects on abundance of species either directly or, more probably, through other inter-related factors. They illustrate how slight environmental variations can lead to the production of patterns in vegetation and to the existence of correlation or association between species. The choice of examples relating micro-topography and the distribution of species by no means excludes the importance of other variable factors which may operate, but it merely underlines the scarcity of data on such inter-relationships.

MODIFICATION OF THE ENVIRONMENT BY ONE SPECIES ALLOWING ESTABLISHMENT BY OTHER SPECIES

Considerable interest was aroused by the publication of a paper by Went in 1942 which demonstrated a marked relationship between the distribution of annual species and perennial shrub species in a desert area in California. His data showed a general positive relationship between shrubs and annual herbs, but a more striking relationship between annual species and dead *Encelia farinosa* bushes than with living bushes. This he suggested was due to the production of a toxic substance by *Encelia* which accordingly limited the herb population closely adjacent to a living individual bush. Gray and Bonner (1948) subsequently isolated such a substance from the leaves of *Encelia*. Later workers in this field have suggested other equally plausible explanations of the phenomenon in terms of the relative build-up of humus content underneath *Encelia* and other species of shrubs. Whatever the causal explanation (see below for a detailed account of the presence of toxic substances in plants) this work did focus attention on the relationship between an individual and its environment and the possible effects of this interaction on other species within the community.

A clear example of this type of relationship taken from stony desert in Iraq is given by Agnew and Haines (1960). There is a considerable deposition of wind-borne material round the base of perennial plants in this area; this leads to the formation of low mounds around the individual shrubs. *Astragalus spinosus* is an outstanding example of this and there is a marked positive correlation between this species and small annual or perennial herbs, both in the sense of abundance as well as luxuriance. A typical cross-section of such mounds is given in Fig. 5.3. *Astragalus spinosus* is a straggling shrub with tough branches and an abundance of sharp spines which are formed from old leaf axes which have hardened after the leaflets have been shed in the summer. These axes remain firmly attached to the woody stems for several years. The relationship is explained by an interaction of several factors which in turn are related to the

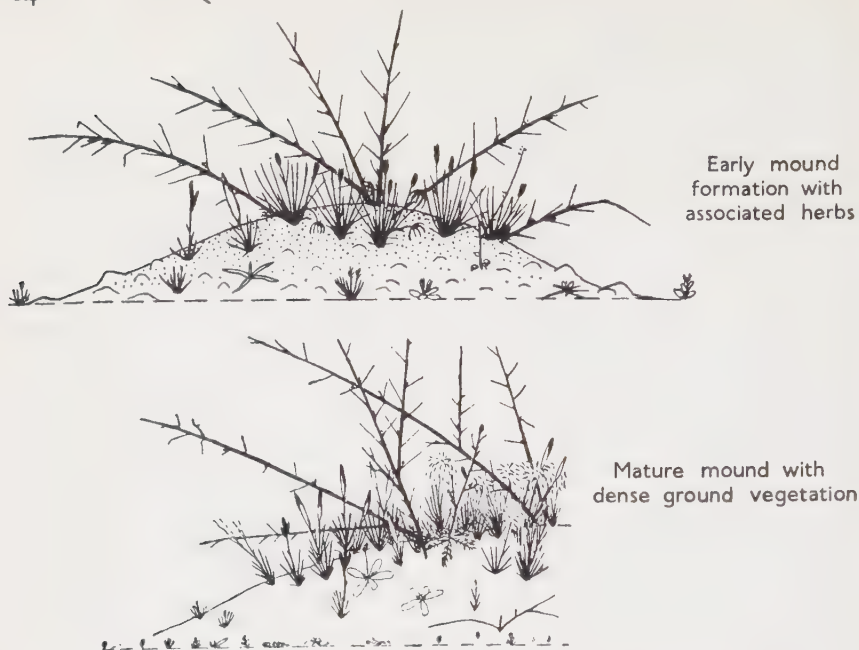


Fig. 5.3. The marked luxuriance and increased abundance of herbaceous species under *Astragalus*. (From Agnew and Haines 1960; courtesy of *Bull. Col. Sci.*)

growth form and general morphology of *Astragalus*. The first important factor is the protection of the associated herb flora from grazing, which is provided by the spiny branches. This factor is of considerable importance in the Middle East where there is very heavy grazing by goats, sheep and camels even in apparently remote desert areas. Grazing will markedly affect both the luxuriance and abundance of individuals of a species. The second factor is the actual presence of wind-borne material which provides a limited area of soil capable of supporting plant growth. The desert area is largely stony and the soil mounds thus provide an excellent site for establishment and growth of herbaceous species. Further increments of debris are added annually; these include plant remains both from the *Astragalus* as well as from the herbaceous cover, thus steadily raising the humus content of the mounds. This has a two-fold effect; the concentration of soil nitrogen is increased and enables a larger population of herbs to exist, and this in turn reduces wind velocity at the surface of the mound. The reduction of wind velocity lowers the rate of evaporation from the soil surface and in effect leads to a more efficient utilisation of the available rainfall.

Thus it is quite clear that the marked association outlined above is dependent on localised variations of several environmental factors, which in turn are related to the existence of a perennial species which has established itself in the first place. This example is clear cut since the environment is so extreme that it approaches the level below which plants cannot maintain themselves, and a slight (advantageous) shift of the environment produces a marked and a readily visible response in the vegetation. Similar relationships will hold in more temperate regions of the world, but here they are much less obvious and little is known about them at present.

The fact that vegetation modifies and changes the environment to a considerable extent is largely responsible for plant succession in general (see Chapter 3). Numerous examples of environmental modification by vegetation are available (e.g. Fig. 3.6, p. 46) and quantitative data are

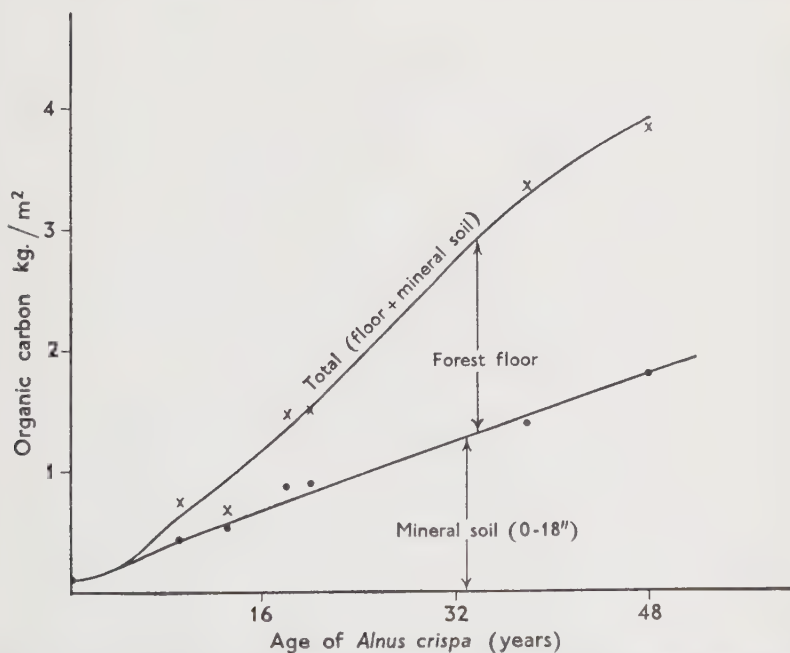


Fig. 5.4. Accumulation of organic carbon in the mineral soil and forest floor under *Alnus crispa* in Alaska. (From Crocker and Major 1955; courtesy of *J. Ecol.*)

given by Crocker and Major (1955) relating the accumulation of organic carbon to the age of a stand of *Alnus crispa* (Fig. 5.4). This accumulation of carbon in a 50-year period and the resultant changes in the vegetation is in fact a characteristic and well marked succession (see Chapter 3, p. 39).

Moreover, this example illustrates the steady build up of humus material in relation to vegetational cover. The rate of build up of humus is of course also dependent to a considerable extent on climate and drainage. Thus in *Astragalus* the nitrogen accumulation will be relatively small, but sufficient to have an effect on the associated vegetation, which leads to the marked positive correlation of species. It is a reasonable assumption that similar effects are present in temperate herbaceous vegetation, but the relative infrequent occurrence of strong positive association between species in this type of vegetation would suggest that such modifications of the environment are often overshadowed by environmental variations resulting from other factors.

PRODUCTION OF TOXIC SUBSTANCES BY PLANTS

As far back as 1832 De Candolle suggested the importance of root excretions and since 1900 considerable attention has been directed towards the detection of substances in plants which are toxic to other species. The demonstration of direct chemical interaction between species is surprisingly difficult, and much of the earlier work designed to prove an interaction between two species based on the exudation of a toxic substance can be criticized on the grounds of experimental design or may be explained in terms of competition for some environmental factor.

Bedford and Pickering (1919) examined in some detail the vigour of apple trees in relation to the grass cover of an orchard. Observation showed a very marked difference between the height and fruit production of trees grown in tilled soil compared with trees of similar age grown in plots with a complete grass cover. For example a plantation of Bramley's Seedling apples established for 23 years was selected and half of it laid down to grass. In the first year the grass did not establish well but even then the season's crop was reduced by 5 per cent (compared with the crop from the tilled section). In the next year the crop was markedly affected as fruit production was reduced by 89 per cent following the complete establishment of the grass. Similar results were obtained in several other experiments, all of which strongly suggested the action of a toxic substance produced by the grass. This possibility was examined further experimentally. Young apple trees were grown in pots while a 'surface crop' of grass was suspended above in a perforated container. Water was supplied through the surface crop which leached any toxic substance into the pot below. The resultant inhibition by the surface crop was very marked in most experiments and amounted to almost complete suppression of tobacco plants by clover and to 40-60 per cent suppression in other experiments.

The results at first sight seem conclusive but the field observations can be explained in part by competition for nitrogen and water. The inhibition

of the trees by grass cover can be almost completely eliminated by addition of nitrogenous fertilizers, together with irrigation of the orchard. The pot experiments are quite convincing, however, and one is forced to conclude that the presence of a toxic substance is probable, but under field conditions it is either destroyed by bacterial action or is absorbed by soil particles. It should, however, be borne in mind that the removal of an inhibitory effect by the addition of nitrogen and water does not necessarily prove that a toxic substance is *not* operative. It could be that the toxic substance produced by the grass for example reduces the root development of the apple trees and accordingly limits their ability to take up nitrogen and water. With the availability of abundant nitrogen and water the limiting effect of a reduced root system is minimal and the apparent toxic effect disappears. In other words the mechanism of competition for nitrogen and water could be through the action of the toxin.

The relationship between apple trees and surface crop illustrates clearly the variety of suggestions that can be offered as an explanation of an observed result. The experiments have to be designed with considerable care, and the above example does emphasize the attendant difficulties in this field of research. More recent work has revealed numerous examples of inhibition of one species by another; these have been usefully reviewed by Bonner (1950) and Woods (1960), and several well documented cases exist of marked inhibition of one species by another where the toxic substance presumably responsible has been isolated and identified. Thus it has been shown that Scopoletin is liberated from oat roots (Martin 1956, 1957, 1958) and that it possesses growth inhibiting properties (Goodwin and Taves 1950; Libbert and Lübke 1957, 1958). Similarly Gray and Bonner (1948) isolated 3-acetyl-6-methoxy-benzaldehyde from leaves of *Encelia farinosa* which was shown to be toxic to tomato and corn seedlings, but it was noted that the toxic effects were far less effective in good garden soil than in sand culture. This suggests an inactivation or destruction of the compound by the soil microflora. The most impressive example is that of *Juglans* (walnut) which has a marked effect on some associated species (Jones and Morse 1903). Under natural conditions it will produce wilting of potato and tomato plants grown in the immediate vicinity (Cook 1921), and has an identified toxic constituent, juglone, present in its roots (Davis 1928). Purified extracts of juglone have produced toxic symptoms in a variety of species investigated so far (Massey 1925, Perry 1932).

It is clear that in many cases toxic substances are produced which will inhibit other species under experimental conditions. However, it is equally clear that usually the activity of the toxin is markedly reduced in soil, probably by the action of soil micro-organisms. Also it is questionable whether sufficient quantities of toxin capable of exerting a measurable effect on associated species are released in the soil. Thus in terms of toxic

substances no conclusive proof exists which would adequately explain positive or (more usually) negative correlations between species. However, the possibility that such a mechanism may operate in some cases at least should not be ignored and the case of *Juglans* (see above) is probably the best available example to date. As has been suggested above, there is considerable difficulty in differentiating under field conditions between a toxic effect and one due to competition. This situation is made even more complex by the possibility that the different competitive ability is actually achieved through the agency of the toxic excretion.

COMPETITION LEADING TO NEGATIVE AND POSITIVE CORRELATION OR ASSOCIATION

The term 'competition' is used in a wide variety of contexts with a slightly different meaning and it has been suggested that 'interference' (Harper 1961) be used as a general term to describe the loss of vigour and productivity of an individual due to the close proximity of another. In this context, however, the term is used to describe the struggle between individuals for some environmental factor such as light or nitrogen, and the final effect is not one of complete elimination of one individual by another but a lowering of the performance of one of the competing members. This is usually manifested in a reduction in the numbers of a plant in relation to another species and leads to a negative correlation between the two.

Much of the detailed work on competition has been carried out under controlled conditions, since in the field it is often difficult to distinguish factors involved in competition from the other possible causes of a negative correlation. In a consideration of effects of competition it is important to realize at which point of the life cycle competition exerts the most pressure, whether it is at the seedling stage or whether the effect is over a longer period of time. The effect of marked competition at seedling stages is usually of greater importance in relation to the actual numbers of plants which survive to maturity. Reduction in numbers of plants is more easily observed in ecological situations than the less obvious effect of reduced performance caused by the close proximity of a competitor. Conversely, in an agricultural or horticultural field, performance and yield are of paramount importance and are related both to plant numbers as well as to the general level of performance of the crop.

An example of the competition between individuals of the same species is given by Harper (1960) who investigated the numbers of mature plants of four species of poppy in sample plots; the numbers resulted from different densities of sown seed. The results (Fig. 5.5) show a clear decline in the number of mature plants relative to the rise in the density of seeds per plot. The density of sown seed produces a corresponding reduction in

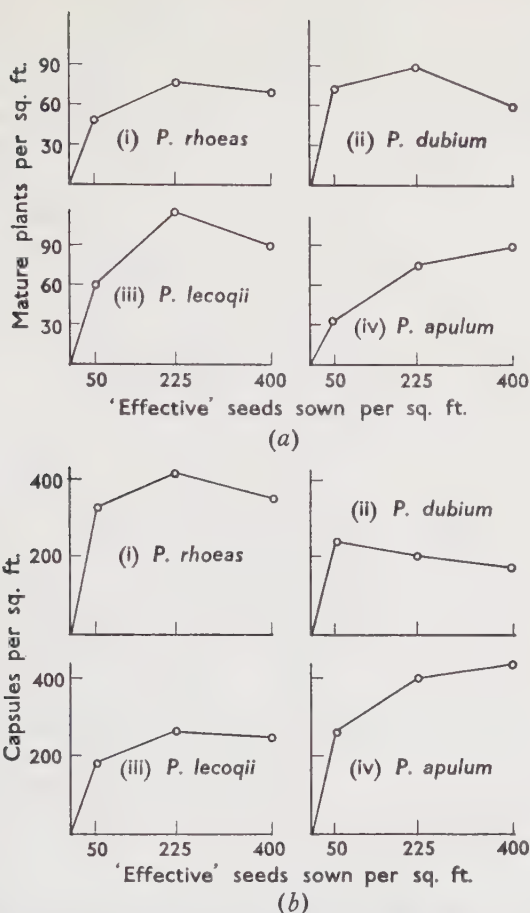


Fig. 5.5. Competition between individuals of the same species, as expressed by number of mature plants per square foot (a), and capsules per square foot; (b), in plots sown with different densities of seed. (From Harper 1960; courtesy of Blackwell Sci. Pub.)

the number of capsules per plant produced by the mature plants. Similarly Donald (1951) (see also Harper 1961) gives data relating the plant weight of *Trifolium subterraneum* to the density of sowing at successive dates (Fig. 5.6). At the time of sowing individual plant weight is of course not dependent on density, but as the plants develop those at the highest density compete for available nutrients and light and show a reduction of plant weight. This effect is seen earliest at high densities but is apparent at progressively lower densities as time goes on and the plants grow larger. These examples show quite conclusively the dependence of plant numbers

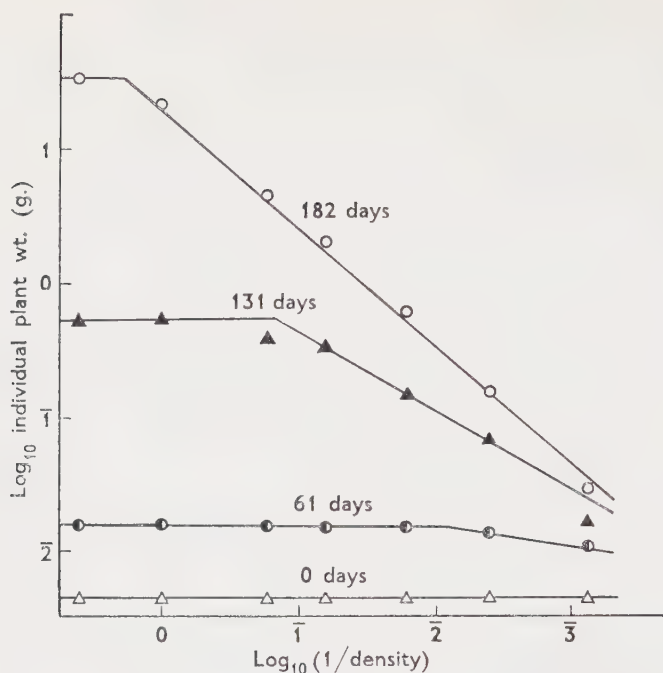


Fig. 5.6. Reduction of individual plant weight by competition between individuals of *Trifolium subterraneum* at different densities and at different times from sowing. (From Harper 1961; courtesy of Cambridge Univ. Press.)

and their performance on initial density of seeds and on the density of mature individuals respectively.

Data showing the effect of different species on the survival of *Juncus effusus* seedlings at different levels of soil fertility are given by Lazenby (1955). Five combinations of species were used: *Juncus* growing alone (J.), *Juncus*, *Molinia caerulea*, and *Trifolium repens* (J.T.), *Juncus* and *Trifolium* (J.T.), *Juncus*, *Trifolium* and *Lolium perenne* (J.T.L.) and *Juncus*, *Trifolium* and *Agrostis tenuis* (J.T.A.). The results are summarized in Fig. 5.7 and all show a marked reduction of both the numbers of plants as well as the performance of *Juncus* in all the competitor combinations used, and at all nutritional levels. Lazenby suggests that the important effects are on the early seedling states of *Juncus* since its seeds require light before they will germinate. Accordingly those species which form a very close sward inhibit germination to a considerable extent.

The examples discussed above are all taken from experiments performed under fairly well controlled environmental conditions, but they all demonstrate the sort of effect which can be expected in natural vegetation. Well documented examples from natural vegetation are few and perhaps

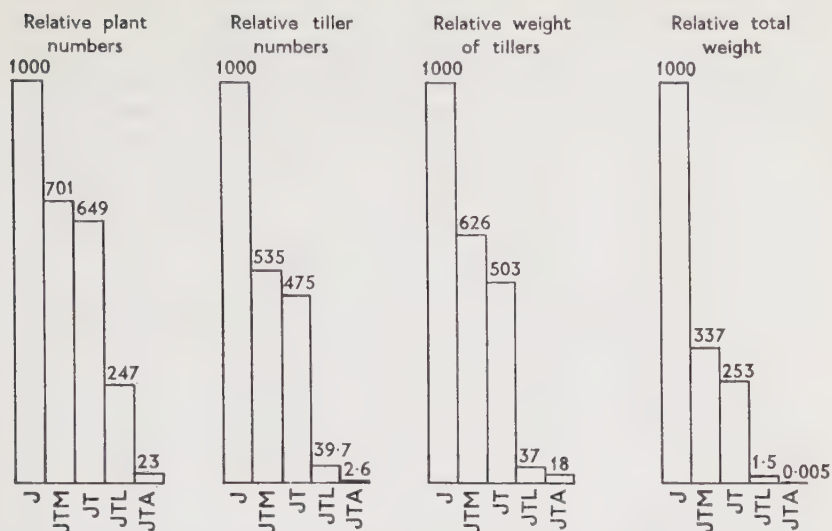


Fig. 5.7. Relative plant numbers, tiller numbers, weight per tiller and total weight of *Juncus effusus* developed with different companion species during 18 months' growth. (From Lazenby 1955; courtesy of *J. Ecol.*)

the most informative data are those relating to the interactions between a tree canopy and the ground vegetation. It is sometimes assumed that the paucity of vegetation beneath trees is a direct result of the low light intensity that prevails at ground level for most of the growing season. This is by no means always correct. Watt and Fraser (1933) examined this relationship in a *Pinus sylvestris* woodland with a ground flora dominated by *Deschampsia flexuosa* and *Oxalis acetosella*, and related the abundance and vigour of these two species to competition with the tree roots for some nutrient factor, possibly nitrogen. The experimental layout consisted of a series of plots surrounded by trenches, which severed tree roots and isolated the herb layer from competition with tree roots at different depths. Five trench depths were used 1-2 in. (raw humus), 3-4 in. (raw humus cut to its entire depth), raw humus plus 4 in. of mineral soil, raw humus plus 8 in. of mineral soil, and raw humus plus 13-18 in. of mineral soil. In addition a control plot, and a series of plots which were not trenched but to which distilled water or nitrogen were added, were also sampled. The plots were sampled prior to trenching and for two years subsequently, after which the experiment was discontinued. The samples were oven dried and the results expressed as percentages of the original crop in each plot. The maximum rooting depths of *Deschampsia* and *Oxalis* were observed to be approximately 24 in. and 3 in. respectively. The majority of the *Pinus* roots were confined to a depth of 3-15 in. A similar series of

experiments were also conducted under beech canopy in an adjacent wood.

The results are summarized in Fig. 5.8 below. In assessing these results note must be taken of the annual reduction of the plot herbage caused by

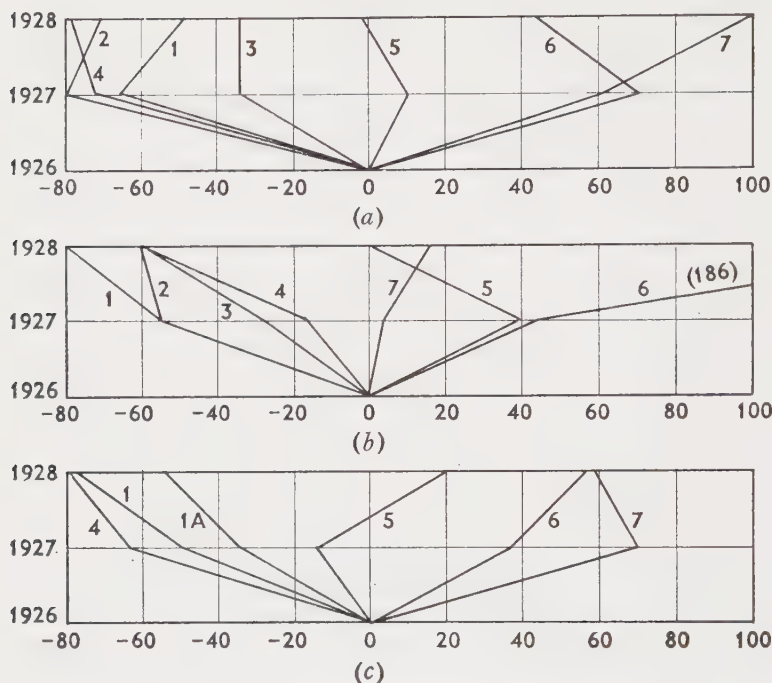


Fig. 5.8. Percentage increase or decrease in the weights of the original field layer of *Deschampsia flexuosa* under pine (a), *Oxalis acetosella* under pine (b), and *O. acetosella* under beech (c). The treatments were: 1. Control. 2. Distilled water added. 3. Raw humus cut 1-2 in. 4. Raw humus cut to surface mineral soil (3-4 in.). 5. Raw humus plus 4 in. mineral soil cut. 6. Raw humus plus 8 in. mineral soil cut. 7. Raw humus plus 13-18 in. mineral soil cut. (From Watt and Frazer 1953; courtesy of *J. Ecol.*)

the actual harvesting. However, they do allow several preliminary deductions to be made. Firstly, the addition of water had no effect on either *Deschampsia* or *Oxalis* (Fig. 5.8, a2 and b2). Secondly, that cutting through the humus and 4 in. of mineral soil and through the main roots of the trees enables both herb species to hold their own and probably in the absence of harvesting they would have actually benefited. Trenching to greater depths shows a general increase in crop weight (Fig. 5.8 (6) and (7)). The addition of nitrogenous fertilisers gave mixed results, *Oxalis* showed no change when the rates of application were small but was completely eliminated by the larger dosage. However, *Deschampsia* benefited

from the small doses although the largest dose had an adverse effect. Thus it appears that nitrogen may be one of the important factors for *Deschampsia* at least, which is limited by tree root competition. Other possible effects of the trenching which should also be noted are that the subsequent death and decay of the severed tree roots would increase the level of nutrient in the soil to a slight extent and also that the decay of the roots would allow greater rates of oxygen diffusion along 'channels' once filled by the roots. The increase in vigour of the herbaceous vegetation is sufficiently large to suggest an increased benefit which is greater than these two possibilities would provide. It is remarkable that the most marked effect on both herb species is at the maximum depth of trenching even though *Oxalis*, for example, has a shallow rooting system.

The inhibition of a stand of trees by the ground vegetation is perhaps, at first sight, surprising, but is a well-known factor in the establishment of certain tree crops and offers a further example of what has been interpreted as competition. One of the more valuable crops planted by the Forestry Commission is Sitka spruce (*Picea sitchensis*), as its yield of timber is high. Early trial plantings showed that spruce planted in *Calluna*, though establishing fairly well, was immediately 'checked' in its growth. Addition of basic slag, as a source of nitrogen and phosphorus improved growth initially, but did not prevent the final onset of 'checking'. The experimental plantings included some mixed stands of Sitka spruce and Scots pine and it was noted that the growth of spruce was greatly assisted by the presence of pine. Weatherell (1957) gives data comparing two stands of equal age (Table 5.3) which show quite clearly the increased growth after 10 years which is even greater after a longer period of time (Table 5.4). This use of a 'nurse' crop is now standard practice. Japanese larch is more commonly used than pine, and the apparent beneficial effect of one tree species on another is related to the presence of *Calluna vulgaris* as a dominant species of the ground layer. Observations

Table 5.3—Comparison of Sitka spruce pure and in mixture with Scots pine at 10 years of age. (From Weatherell 1957; courtesy of *Quat. J. Forestry*)

	Pure plantation (Sitka spruce)		Mixed plantation (Sitka spruce and Scots pine)	
	Mean height spruce (feet)	Mean growth 1937 (inches)	Mean height spruce (feet)	Mean growth 1937 (inches)
Not manured	1.8	1.4	2.4	4.1
Basic slag applied shortly after planting	2.6	3.4	3.2	6.6

Table 5.4—Comparison of Sitka spruce pure and in mixture with Scots pine at 12 years of age. (From Weatherell 1957; courtesy of *Quat. J. Forestry*)

	Pure plantation spruce		Mixed plantation spruce and pine	
	Mean height (feet)	Mean growth 1939 (inches)	Mean height (feet)	Mean growth 1939 (inches)
Not manured	2.0	1.7	3.2	6.4
Basic slag applied after planting	3.1	2.8	4.2	7.0

show that the roots of spruce growing adjacent to Japanese larch tend to be very much more developed under the larch than in the area dominated by *Calluna* and tend to run in the larch needle litter, only rarely descending into the mineral soil. Japanese larch very effectively suppresses *Calluna* and concurrently with the removal of this competition spruce will grow at a greater rate than a pure stand which only slowly suppresses *Calluna*. It seems likely that the roots of larch and spruce occupy different levels in the soil and accordingly any competition between them is minimized. The effect of Japanese larch as a nurse crop is well marked (Table 5.5), the height of spruce being doubled over a period of 13 years. The beneficial effects of basic slag suggest that nitrogen (the addition of

Table 5.5—Height in feet of various species mixtures after 13 years. (From Weatherell 1957; courtesy of *Quat. J. Forestry*)

Crop	Height of spruce (feet)	
	Complete ploughing	Single furrow ploughing
Three rows of spruce alternating with two rows of Japanese larch	13.2	12.4
Sitka spruce plus broom	13.3	9.0
Two rows of spruce alternating with two rows Scots pine	9.4	8.5
Alternating rows of spruce and pine	10.5	10.6
Two rows of spruce alternating with single row Scots pine	7.5	8.5
Pure stand spruce	6.0	6.0

calcium accelerating nitrification) or phosphorus or both are possible requisites in the competition interaction between spruce and *Calluna*; however, other factors may well be involved.

The relationship between the ground layer and tree layer outlined above demonstrates a presumed competition between the two life forms. None of the results is conclusive and the same difficulty exists in attempting to relate the observed effect with a causal mechanism. That is to say, it seems a reasonable assumption that the observed increase in vigour in these instances is directly related to the removal of competition, but it can be argued that an identical effect would be produced by the removal of the source of an inhibitory substance. This is the converse of the problem outlined above (p. 87); when the results of controlled experiments are extrapolated into field conditions the definition of causality is immediately open to several explanations unless the data is obtained by extremely critical sampling of both vegetation and environment. Due to the time factor, such sampling presents considerable difficulty, even if one assumes that soil analyses can be done to the required order of accuracy; this latter difficulty at the moment appears insurmountable.

6 The Poisson Series and the Detection of Non-Randomness

INTRODUCTION

IN addition to the detection of non-randomness in species distributions by correlation methods discussed in the last chapter, a number of approaches have been made to the non-random distribution of individuals of the same species. This, in part, can be accounted for in similar terms as correlation between species, but several other methods of detecting departure from randomness are available.

HISTORICAL

The earliest accounts of the non-random nature of the distribution of plants in a community are those of Gleason (1920) and Svedberg (1922) who independently showed that several species were markedly non-random. Svedberg's approach to the problem has since become one of the standard methods of detecting non-randomness in vegetation and consisted of relating the observed number of individuals per quadrat to the expected number derived from the Poisson series e^{-m} , $m e^{-m}$, $m^2/2! e^{-m}$, $m^3/3! e^{-m}$, $m^4/4! e^{-m}$, . . ., where m is the mean density of individuals. Successive figures of the series give the probability of quadrats containing 0, 1, 2, 3, 4, . . . individuals respectively, and the expected number of quadrats thus falling into each of these classes can be readily calculated. The nature of the non-randomness was termed as 'overdispersed' when individuals tended to be clumped together, and 'underdispersed' when individuals were scattered very evenly over the area. Overdispersion is thus characterized by large numbers of both empty quadrats and quadrats containing a large number of individuals, and similarly underdispersion by the majority of quadrats containing an intermediate number of individuals. Svedberg showed that dispersal of a number of species agreed satisfactorily with the Poisson series which indicated random dispersion, but also that several species showed either 'overdispersion' or 'underdispersion'. The terms 'overdispersed' and 'underdispersed' refer to the distribution curve of the data and *not* to the pattern of individuals on the ground. This has led to some confusion and it has been suggested by

Greig-Smith (1957) that the terms 'contagious' and 'regular' should replace 'overdispersion' and 'underdispersion'. In a Poisson series the variance is equal to the mean and thus the ratio of these two values is equal to 1. Svedberg used this ratio as a measure of randomness; when the values were greater than 1 the distribution was assumed to be contagious, when less than 1 it was assumed to be regular.

TESTS OF SIGNIFICANCE

The use of variance:mean as an index of contagion in vegetation has since been used by a number of workers (Clapham 1936, Archibald 1948, Dice 1948, etc.) usually employing a significance test for the difference between the observed and expected variance:mean ratio (Blackman 1942) or a χ^2 -test to compare the terms of the Poisson series with the observed data (Blackman 1935). In addition to the test of goodness of fit, and variance:mean ratio (sometimes termed the Coefficient of Dispersion (Blackman 1942) or relative variance (Clapham 1936)) several additional tests for non-randomness have been devised which are adequately described by Greig-Smith (1957) (see also Moore 1953, Ashby, 1935, David and Moore 1954, Whitford 1949) and are not discussed here. However, as Evans (1952) has pointed out the variance:mean ratio may give a widely different estimate of non-randomness from a χ^2 -test of goodness of fit and it may be necessary to use more than one test for non-randomness. Evans gives the following hypothetical case with a mean and variance of 1.00 and hence a variance:mean ratio of 1 which indicates a random distribution within the population:

Table 6.1—The observed and expected number of quadrats containing 0, 1, 2, ... individuals in a hypothetical case, where the variance and mean of the population equal 1

Number per quadrat	Observed number of quadrats	Expected number of quadrats
0	20	37.16
1	76	37.16
2	—	18.58
3	—	6.19
4	—	1.55
5	5	0.31
> 5	—	0.05

Obviously there is a considerable discrepancy between the observed and expected data ($\chi^2 = 63.24$, $p \ll 0.1$ per cent) and in general the χ^2 -test of goodness of fit is a more reliable indication of non-randomness than the variance:mean ratio.

The method of testing departure from randomness is illustrated below. The data are taken from two communities, one consisting entirely of random individuals (Fig. 6.1) and one with hypothetical offspring grouped around the 'parents' (Fig. 6.2). The data has been obtained from randomly

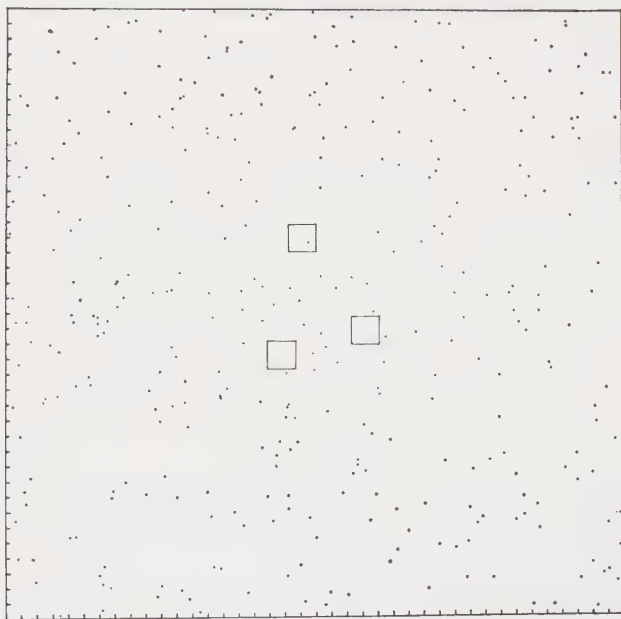


Fig. 6.1. A random 'community' with sample quadrats positioned by pairs of random co-ordinates.

placed quadrats located by pairs of co-ordinates, taken from tables of random numbers. Thus the first quadrat is located by co-ordinates 240.200 (the bottom-left hand corner of the quadrat), the second by co-ordinates 163.187 the third 179.241 and so on (a procedure identical with that used to position the 'individuals' (Fig. 6.1) in the 'community'.

1. RANDOM POPULATION (Fig. 6.1)

The data for 100 random samples is given below:

Table 6.2—The observed number of quadrats containing 0, 1, 2, . . . individuals taken from a random population

Number of individuals in each quadrat (<i>a</i>)	0	1	2	3
Frequency of occurrence in 100 quadrats (<i>f</i>)	46	34	14	6

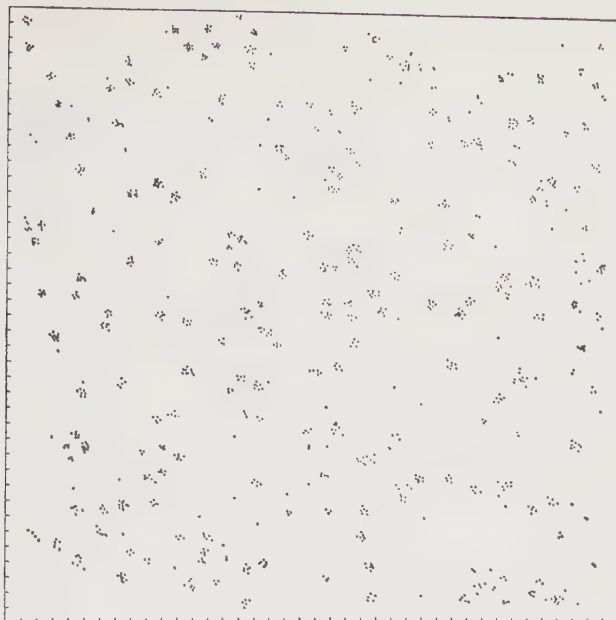


Fig. 6.2. A contagious distribution of individuals.

(a) χ^2 goodness of fit

$$\text{Mean density of the population, } m = \frac{Saf}{100} = 0.8$$

Thus from the series e^{-m} , $m e^{-m}$, $\frac{m^2}{2!} e^{-m}$, $\frac{m^3}{3!} e^{-m}$, ..., the expected number of quadrats containing 0, 1, 2, ... individuals can be calculated:

$$e^{-m} = e^{-0.8} = 0.4493$$

(see Greig-Smith 1957; Appendix B, Table 3)

$$m e^{-m} = 0.4493 \times 0.8 = 0.3594$$

$$\frac{m^2}{2!} e^{-m} = 0.4493 \times \frac{0.64}{2} = 0.1438$$

$$\frac{m^3}{3!} e^{-m} = 0.4493 \times \frac{0.512}{6} = 0.0383$$

Thus the expected distribution should be:

$$0.4493 \times 100, \quad 0.3594 \times 100, \quad \dots \text{ and thus:}$$

Number of individuals per quadrat	0	1	2	3
Expected frequency	44.9	35.9	14.4	3.8
Observed frequency	46	34	14	6
Difference	1.1	1.9	0.4	2.2

The goodness of fit is calculated as the sum of the differences squared divided by the expected frequency:

$$\begin{aligned}
 &= \frac{(1.1)^2}{44.9} + \frac{(1.9)^2}{35.9} + \frac{(0.4)^2}{14.4} + \frac{(2.2)^2}{3.8} \\
 &= 0.0269 + 0.1006 + 0.0111 + 1.2737 \\
 &= 1.4123
 \end{aligned}$$

The χ^2 -table is entered with 2 degrees of freedom (2 less than the number of terms used to calculate the χ^2 total) which shows a value of 1.386 when $p=0.5$. Thus the chance of this difference between the two sets of data arising fortuitously is 50:50 and we can regard the observed data as showing a very good fit with the expected series and the population sampled was randomly distributed. (When the chance of a difference between two sets of figures arising completely fortuitously, falls as low as 0.05 (1 in 20 or a 5 per cent level of significance) it is usually considered that such a level of odds necessitates some other hypothesis, and the difference can be safely regarded as 'real' rather than 'accidental').

(b) *Variance : Mean ratio*

From the data above:

$$\begin{aligned}
 N &= 100, \quad \bar{x} = \frac{S(x)}{N} = \frac{80}{100} = 0.8 \\
 S(x)^2 &= 144 \\
 (Sx)^2 &= 6400 \\
 \therefore \frac{(Sx)^2}{N} &= 64.
 \end{aligned}$$

The variance of the population is given by

$$\frac{S(x)^2 - \frac{(Sx)^2}{N}}{N-1} = \frac{144 - 64}{99} = \frac{80}{99} = 0.8080$$

$$\text{Thus the variance:mean ratio} = \frac{0.8080}{0.8000} = 1.01$$

The variance:mean ratio shows the population to have apparently some degree of contagion, and this difference from the expected ratio of 1 must be tested by a *t*-test:

Standard error of the variance:mean ratio is given by

$$\begin{aligned}
 \sqrt{[2/(N-1)]} &= \sqrt{\frac{2}{99}} = 0.1421 \\
 t &= \frac{\text{Observed} - \text{Expected}}{\text{Standard Error}}
 \end{aligned}$$

$$= \frac{0.01}{0.1421}$$

$$t = 0.0704, p < 0.9$$

Again this difference is not significant for such a difference could arise by chance very frequently, and the distribution of the population can be regarded as random.

II. CONTAGIOUS POPULATION (Fig. 6.2)

The data for 100 random samples is given below, the sampling procedure being identical to that used above:

Table 6.3—The observed number of quadrats containing 0, 1, 2, . . . individuals taken from a contagious population

Number of individuals in each quadrat	0	1	2	3	4	5	6	≥ 7
Frequency of occurrence in 100 quadrats	47	6	5	8	5	6	7	16

(a) χ^2 goodness of fit

Mean density of the population, $m = 2.44$

The Poisson series with this mean value is given by the probabilities:

$$e^{-m} = e^{-2.44} = 0.0872$$

$$m e^{-m} = 0.2128$$

$$\frac{m^2 e^{-m}}{2!} = 0.2596$$

$$\frac{m^3}{3!} e^{-m} = \frac{2.44^3}{6} 0.0872 = 0.2111$$

$$\frac{m^4}{4!} e^{-m} = \frac{2.44^4}{24} 0.0872 = 0.1288$$

$$\frac{m^5}{5!} e^{-m} = \frac{2.44^5}{120} 0.0872 = 0.0628$$

$$\frac{m^6}{6!} e^{-m} = \frac{2.44^6}{720} 0.0872 = 0.0256$$

$$\frac{m^7}{7!} e^{-m} = \frac{2.44^7}{5040} 0.0872 = 0.0089$$

Number of individuals per quadrat	0	1	2	3	4	5	6	>7
Expected frequency	8.7	21.3	26.0	21.1	12.9	6.3	2.6	0.9
Observed frequency	47	6	5	8	5	6	7	16
Difference	38.3	15.3	21.0	13.1	7.9	0.3	4.4	15.1

$$\chi^2 = \frac{(38.3)^2}{8.7} + \frac{(15.3)^2}{21.3} + \dots + \frac{(15.1)^2}{0.9}$$

$$= 470.334, \quad p < 0.001$$

The difference between the observed and expected numbers of occurrences is highly significant, the chances of this difference arising accidentally are very much greater than 1,000:1.

(b) *Variance: mean ratio*

$$N = 100, \quad m = \bar{x} = 2.44$$

$$S(x)^2 = 1.364$$

$$(Sx)^2 = 59,536$$

$$\frac{(Sx)^2}{N} = 595.36$$

$$\frac{S(x^2) - \frac{(Sx)^2}{N}}{N - 1} = \frac{768.64}{99} = 7.7640$$

$$\therefore \text{Variance: mean ratio} = \frac{7.7640}{2.44} = 3.182$$

$$\text{Standard error} = 0.1421$$

$$\therefore t = \frac{2.182}{0.1421}$$

$$= 15.3554 \text{ with } 99 \text{ degrees of freedom, } p < 0.001$$

Again the probability of this difference arising by chance is very much less than 1000:1.

Various criticisms of the variance: mean ratio have been made, in addition to the case outlined by Evans (1952) described previously. Thus Jones (1955-6) suggests the interpretation of variance: mean ratios is very unreliable when the mean density of individuals is very high or very low, and Skellam (1952) has criticized this approach on the grounds that the success of the ratio as an indicator of non-randomness is dependent on the size of the quadrat used for sampling. This latter criticism, is, in fact, applicable

to all of the methods used in the detection of non-randomness of vegetation. This effect of size of quadrat can be very useful in gaining information on the scale of the non-randomness present and is discussed below. In general the χ^2 -test for goodness of fit gives a reliable indication of the occurrence of non-randomness relative to the choice of quadrat size, provided very abundant and very rare species are not included in the investigation. Both these tests and others which have appeared are not applicable to distributions where an individual is not an obvious entity, and work on grassland for instance has accordingly been severely handicapped (see below).

Several attempts at deriving a method for detecting non-randomness in the distribution of tree species have been made. These have involved measures of point-to-plant and plant-to-plant distances.

Basically all the methods employing distance measures between individuals or between random points and individuals depend on the relationship between these measures in a random population. Thus when individuals are distributed at random, the ratio of mean distance from a random point to the nearest individual, to the mean distance between randomly selected individuals to its nearest neighbour, should be unity. This ratio will be greater than one when individuals are contagiously distributed and less than one when they are evenly distributed (corrected for the relative density of individuals). The significance of departure from expectation can be tested in a variety of ways.

CONTAGIOUS DISTRIBUTIONS

Following the demonstration that the observed distribution of individuals in a plant community did not fit a Poisson series, a considerable effort was made to find some mathematical series to which field data of this nature could be satisfactorily fitted. The type of function used in all cases involves parameters relating the distribution of individuals to random central points, around each of which a number of 'offspring' is scattered. Thus contagious distribution of individuals is related to the most obvious and likely causal factor—that of vegetative spread or heavy seeds from a parent individual the parents being distributed at random. Archibald (1948, 1950) found a satisfactory fit for many (though not all) species, to Neyman's contagious distribution and also to a similar distribution Thomas's Double Poisson. Similarly, Barnes and Stanbury (1951) found a satisfactory fit to Neyman's and Thomas's distributions using data taken from uniform deposits of china clay residues in the process of being colonized. On the other hand, Thomson (1952) found only one species out of three tested that fitted these distributions at all satisfactorily. Several other distributions have been suggested, based on the pre-

mise that contagion in vegetation is largely due to the morphology of the individual or the efficiency of seed dispersal mechanisms, and operates at one (small) scale only. Unfortunately the value of this approach is minimized by two considerations: (a) later work has shown that contagion in vegetation is due to a multitude of factors and is present on numerous scales in any one site; (b) the mathematical parameters employed to define the distribution and generate the series have no meaning ecologically, or at least it is impossible to relate known ecological factors to these parameters. Thus whilst the approach is of considerable academic interest to the mathematician it is of little use to the ecologist and it would appear that the complexity and variation in the distribution of individuals is of such an order that the formulation of a mathematical model is virtually impossible and it is necessary to fall back on rather simpler empirical approaches.

THE EFFECT OF QUADRAT SIZE ON THE DETECTION OF NON-RANDOMNESS

One of the criticisms made of the variance:mean ratio and goodness of fit as tests of non-randomness in vegetation, has been the dependence of its detection on quadrat size (Skellam 1952). On theoretical grounds it can be readily shown that in any contagious population the use of a Poisson series and tests of departure from it will show both random, contagious and regular distribution as the size of quadrat is steadily increased. This is illustrated below (Fig. 6.3) where sampling with quadrats *A* or *B* the

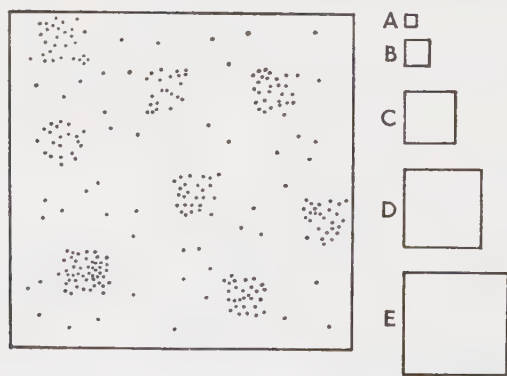


Fig. 6.3. The relationship between quadrat size and variance (see text).

population would probably show slight contagion, sampling with quadrat *C* very marked contagion (each quadrat would contain very many or very few). With quadrats *D* and *E* the distribution would appear to tend towards a regular distribution with all quadrats containing approximately

the same number of species. Thus the most marked demonstration of contagion would be with the quadrat with an area approximately equal to the area of the clump.

Greig-Smith (1952) gives data obtained from a series of artificial layouts of coloured discs, and some of the data is presented below (Table 6.4), which illustrates the apparent change of distribution of individuals in a population with increase in size of the sampling unit. For quadrat sizes 10, 15, 20 and 25 cm there is a marked indication of randomness; at 30 cm the relative variance (variance:mean ratio) increases sharply to a significant level which is maintained in the 35 and 40 cm quadrats, indicating the contagious nature of the artificial population.

(The relationship between quadrat size and variance can be readily appreciated from the hypothetical scheme above (Fig. 6.3). With the small quadrat *A* roughly equal proportions of the quadrats will contain high, intermediate and low densities of individuals. With quadrat *C* on the average high or low values will predominate and the variance accordingly will be high. Finally, a very large quadrat (*E*) will contain roughly equal numbers of individuals and the variance of the data will be very low.)

Table 6.4—Density data from Experiment 5 (Mosaic of irregularly shaped areas), showing the change of contagion detected with increase of quadrat size. (From Greig-Smith 1952; courtesy of *Ann. Bot., Lond.*)

Quadrat size	Mean	Mean per 100 cm ²	Variance: Mean ratio	<i>t</i>	<i>p</i>	χ^2	<i>n</i>	<i>P</i>
10 cm	0.07	0.07	0.9394	0.43	0.6-0.7	—	—	—
15 cm	0.18	0.08	1.0527	0.37	0.7-0.8	—	—	—
20 cm	0.29	0.07	0.9958	0.03	0.9	—	—	—
25 cm	0.39	0.06	1.1342	0.94	0.3-0.4	1.56	1	0.2-0.3
30 cm	0.68	0.08	1.3928	2.76	0.001-0.01	4.00	1	0.02-0.05
35 cm	0.79	0.06	1.5674	3.99	0.001	2.29	1	0.1-0.2
40 cm	0.97	0.06	1.6340	4.46	0.001	26.14	2	0.001

The χ^2 goodness of fit gives a closely comparable picture but it does not reach a significant level of departure from expectation until the 40 cm sampling quadrat. The approximate area of the 'mosaic' employed of high and low densities in this particular layout corresponds more or less with the 35-40 cm quadrat.

The importance of the relationship between quadrat size and detection of contagion lies in the fact that the actual scale at which clumping occurs can be detected merely by resampling the population several times with different sizes of quadrats. Since non-randomness may thus be demonstrated in vegetation where a close visual inspection does not reveal any obvious sign of clumping, this is an important step forward. The mere

demonstration of non-randomness in vegetation is of very limited interest but once information is available as to the scale or scales at which this non-randomness occurs, it becomes possible to relate some environmental factor or factors to scales of the detected non-randomness.

THE ANALYSIS OF A CONTIGUOUS GRID OF QUADRATS AND THE DETECTION OF PATTERN

The development of the analysis of a grid of quadrats is a logical step following the demonstration of the dependence of the detection of non-randomness on quadrat size. Instead of throwing a range of quadrat sizes over an area, a grid of contiguous quadrats is laid out and enumerated, the increasing 'quadrat' sizes then being built up by blocking adjacent quadrats in pairs, fours, eights, etc. An analysis of variance of the data is then carried out, the variance being partitioned between the different block sizes. In the graph relating the mean square (variance) to block size the different scales of pattern appear as peaks at a block size corresponding to the mean area of 'clump'. As was pointed out above, this approach is normally used where no visual contagion (pattern) is detected and the term 'clump' is, more strictly speaking, an area where a species is at a slightly higher or lower density than in the surrounding area. This slight difference in density is not apparent on a visual inspection.

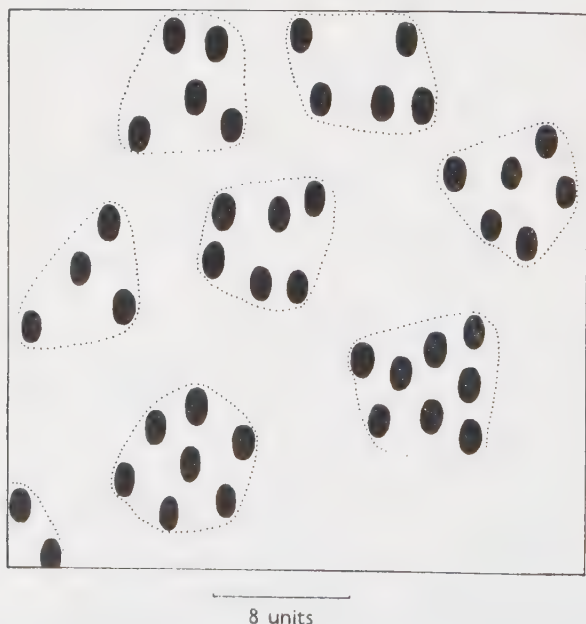


Fig. 6.4. An artificial 'community' with two scales of pattern (see text).

An example of such an analysis is given below with data taken from an artificial layout of clumps 2 units square grouped into a second scale of pattern at 64 units (Fig. 6.4). The analysis of variance table (Table 6.5) and graph of mean square against block size (Fig. 6.5) shows very clearly the two scales of pattern present in the layout as a double peak.

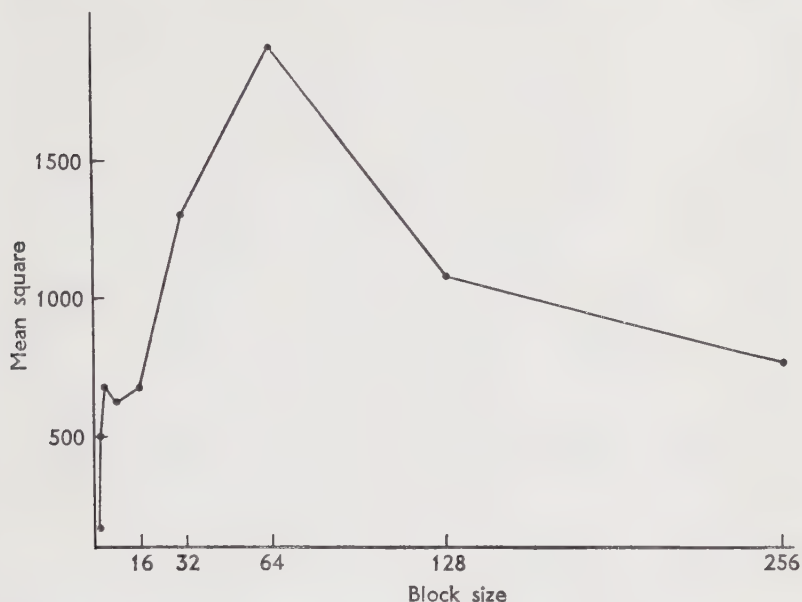


Fig. 6.5. Mean square (variance)/block size graph with a double peak representing two scales of pattern (see text).

Table 6.5—Analysis of variance for data taken from an artificial layout with two scales of pattern

Block size (N_s)	(Sx^2)	$\frac{(Sx^2)}{N_s}$	Sum of squares	Degrees of freedom	Mean square (variance)
1	483,867.45	483,867.450	84,709.815	512	165.449
2	798,315.27	399,157.635	129,738.643	256	506.792
4	1,077,675.97	269,418.992	88,065.841	128	688.014
8	1,450,825	181,353.151	40,492.551	64	632.696
16	2,253,769.61	140,860.600	21,728.739	32	679.023
32	3,812,219.57	119,131.861	21,025.536	16	1,314.096
64	6,278,804.81	98,106.324	15,293.160	8	1,911.645
128	10,605,382.63	82,813.165	4,337.279	4	1,084.320
256	20,089,826.77	78,475.886	1,537.425	2	768.712
512	39,392,492.49	76,938.461	93.431	1	93.431
1024	78,689,318.49	76,845.030	—	—	—

The original method entailed using density as a measure of abundance but the approach was modified and extended (Kershaw 1957) to enable percentage frequency or cover data to be used when the technique was being applied to grassland communities, etc. Frequency can be very readily utilized in this type of analysis, the basic unit of the grid being a sub-divided quadrat instead of a simple quadrat. Presence or absence is recorded for each sub-division of the basic grid unit (25 sub-divisions are usually sufficient) and a percentage frequency figure calculated for each quadrat in turn of the whole grid. The frequency data are then blocked up as before and analysed, the graph mean square/block size peaking at the mean area of 'clump'. The conversion of the technique to cover data necessitates a change of approach in that instead of detecting the mean *area* of a 'clump' a line of cover readings is taken and analysed giving the mean *dimension* of a scale or scales of pattern. A Perspex frame has been designed to enable contiguous cover readings to be taken at intervals as small as 1 cm along a transect (Fig. 6.6). Thin needles are lowered, or optical measure taken (by sighting through the two sets of holes on to the ground layer) and recorded, down one edge of the frame. The frame is then pivoted and the readings continued along the next row of holes that have thus been brought into line. Each set of five adjacent readings are grouped together and expressed as a percentage cover reading. The cover readings are then blocked up and analysed, the peaks in the graph representing the mean *dimension* of a scale of pattern.

Originally it was thought necessary to transform the data before analysing it but it appears that this is not essential (Greig-Smith 1961a) unless tests of significance are to be made. The significance of any particular peak represents a difficulty that was finally overcome by a subjective approach. Under non-random conditions the use of a variance ratio test is invalidated and it was therefore necessary to fall back on the consistent appearance of a peak in a set of replicates. Thus if in a series of replicate samples two scales of pattern are detected at the same or closely similar block sizes in all the analyses, they can be taken as certain departures from randomness at these two scales. Thompson (1958) has considered the statistical implications of the method and also suggests repeated sampling of a population will distinguish chance effects from steady trends inherent in the community. The general reliability of this approach has been tested by trials on artificial layouts of different types (Kershaw 1957). In general as long as the basic unit is smaller than the smallest scale of pattern to be detected, the abundance of the species being investigated is not too low and some degree of replication is obtained, the results are reliably consistent (see also Greig-Smith 1961a).

It is more usual to adopt the dimensional approach even when using density data, since it is easier to obtain rapidly a clear picture of the

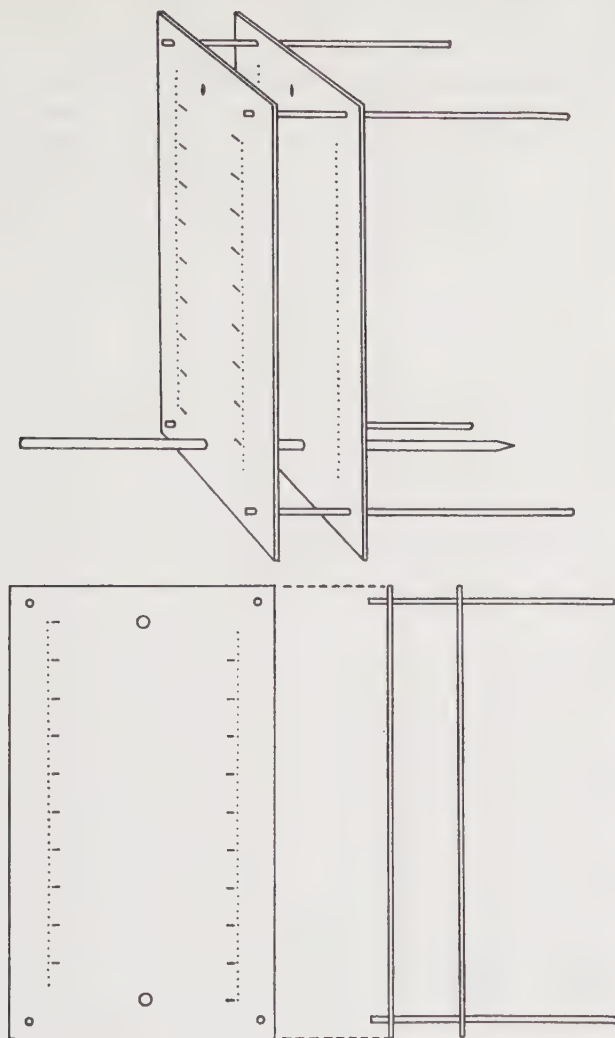


Fig. 6.6. A point quadrat for taking contiguous cover readings along a transect. (From Kershaw 1958; courtesy of *J. Ecol.*)

dimension of the scales of pattern present with four transects of quadrats than it is to add more rows of transects to build up a complete grid. Numerous examples are available of various patterns in vegetation that have developed in response to certain factors and it is clear that the technique is more than sufficiently sensitive to detect very faint pattern.

The use of this approach to non-randomness in vegetation does enable a detailed approach to be made to the causal factors underlying the pattern (see below). When a pattern is very slight it is likely that one or relatively few environmental factors will be controlling it. Conversely, if a

pattern is very marked, it is probable that a number of environmental factors are involved. In the former case it is often possible to make an approach to the causal factor involved, in the second instance the factors are often so numerous as to defeat any attempt at elucidating their effects and interactions. Similarly where a pattern is clearly visible without recourse to detailed statistical analysis, the complexity of the environmental background of such patterns is too great to enable a clear insight into the detailed mechanism. Thus a study of pattern is of considerable use in

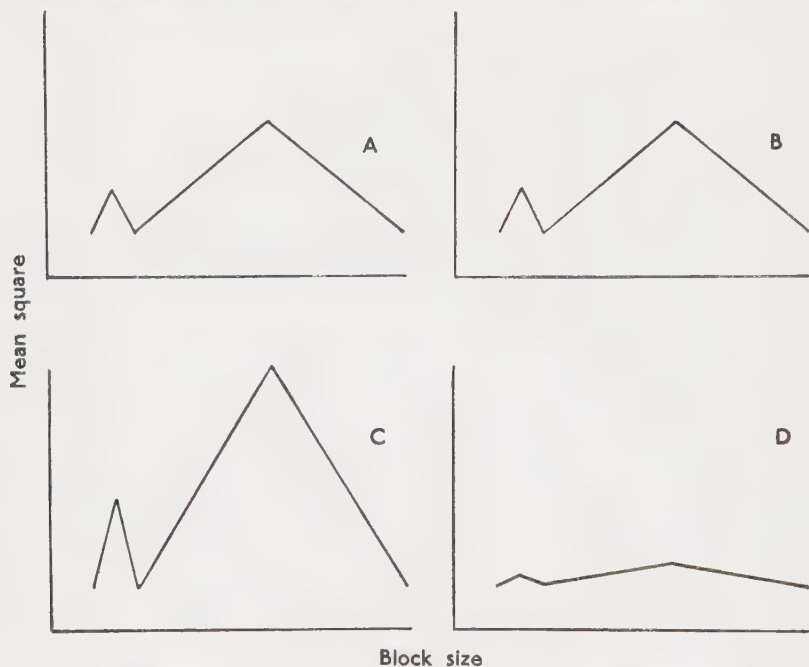
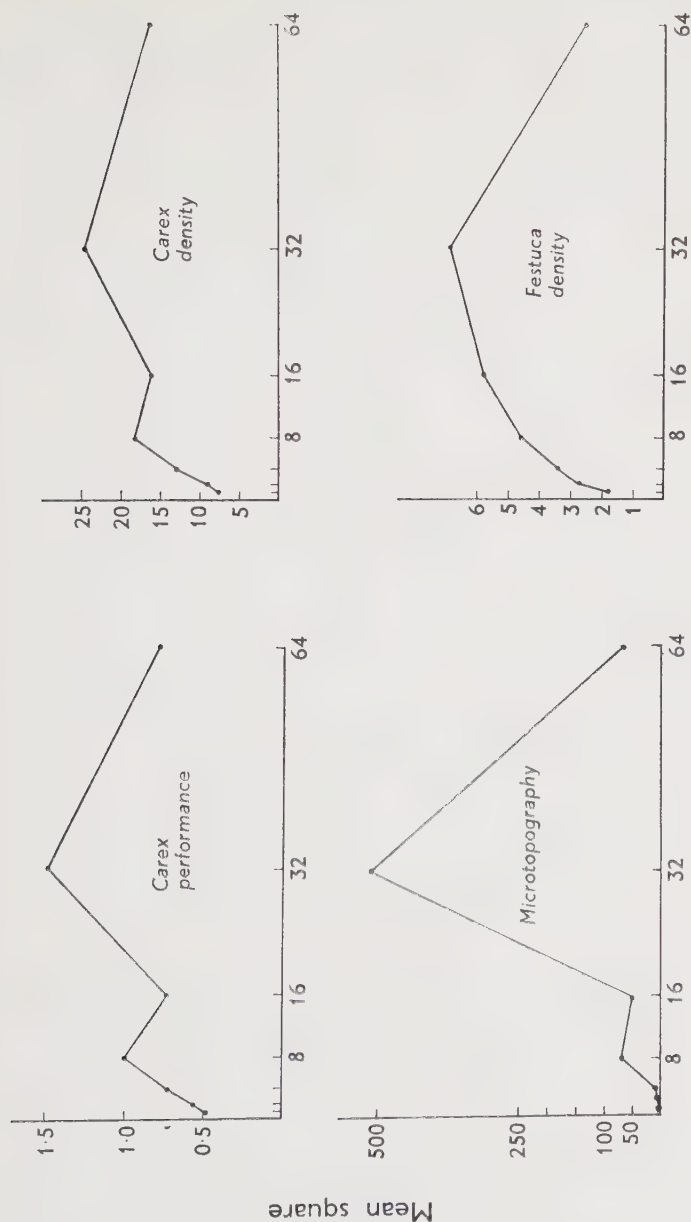


Fig. 6.7. *A* and *B* represent hypothetical patterns of two species when analysed separately. If analysed jointly their pattern will be as *C* if they are positively associated and as *D* if negatively associated.

studies of interactions between the environment and vegetation and also between individual and individual. Pattern can similarly be expressed as a level of association between species (see an earlier section) and in fact the trend of association between species is often of considerable use in gaining an understanding of the causal factors of the pattern. Thus once two species are positively or negatively related in a community, the population will be non-random and the pattern thus present can be expressed either as an analysis of variance or as a correlation coefficient.

The relationship between quadrat size and the trend of detected association discussed in an earlier section, is very marked in the variance analysis.



Block size

Fig. 6.8. The scales of pattern in *Carex bigelowii*, *Festuca rubra* and microtopography in an Icelandic *Rhacomitrium* heath. (From Kershaw 1962; courtesy of J. Ecol.)

Correlation coefficients similarly can be calculated for different block sizes and the change of trend of association related to the scales of pattern of the species. A single approach to this aspect of non-randomness can be made by considering the covariance between two species and analysing it in a similar way to variance (Kershaw 1960). Thus if two species *A* and *B* are not related in any way then $\text{Var } A + \text{Var } B = \text{Var } (A + B)$. Conversely if they are associated in some way, the observed variance will be different from the expected variance. This is conveniently illustrated by considering

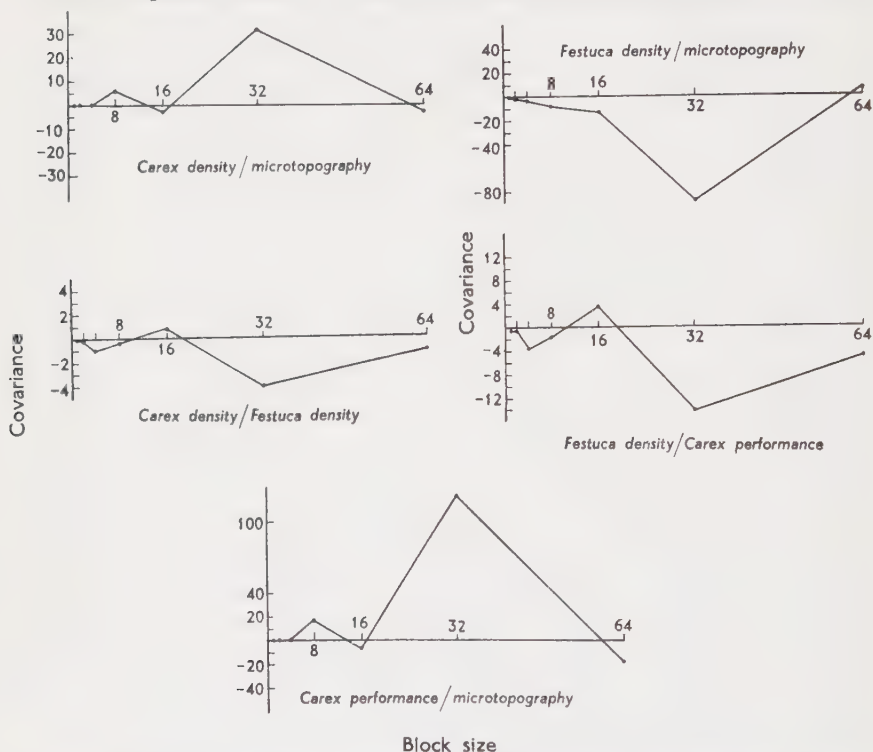


Fig. 6.9. The relationships between *Carex* density, *Carex* performance, *Festuca* density and microtopography, expressed as covariance (see text). (From Kershaw 1962; courtesy of *J. Ecol.*)

two species *A* and *B* having two scales of pattern as shown above in Fig. 6.7 *a* and *b*. If they are associated together positively then the analysis of the joint data of *A* and *B* (i.e. the original data of *A* added to the original data of *B*) will show an increase of variance over and above that expected on theoretical considerations (Fig. 6.7c). Similarly if *A* and *B* are negatively related, the joint analysis of *A* and *B* will show a decrease of variance compared with that expected (Fig. 6.7d). The difference between the

observed mean square/block size graph for *AB* and that expected (i.e. the mean square/block size graph of *A* plus that of *B*) is a measure of the co-variance between *A* and *B* at different block sizes. An example is given above showing the relationship between *Carex bigelowii* and *Festuca rubra* in *Rhacomitrium* heath in Iceland (Kershaw 1962) (Fig. 6.8). The microtopography of the area shows two scales of pattern at block size 8 and 32 (equivalent to 80 cm and 32 m). The density and performance data (expressed as mean leaf length per quadrat of *Carex*) show an identical pattern which immediately suggests a correlation with the microtopography of the area. The variance analysis of the density data for *Festuca rubra* is not as clear cut, apparently lacking the primary peak at block size 8 but having a marked peak again at block size 32. The co-variance analyses (Fig. 6.9) confirm the suspected relationship between microtopography and the distribution of *Carex*. Both *Carex* density and *Carex* performance are obviously positively correlated with microtopography and it is interesting to note the amplitude of the peak for performance/microtopography is greater than density/microtopography. This is a clear indication that the performance of *Carex* is affected more markedly by microtopography than is the density. *Festuca* and *Carex* are shown to have a markedly negative correlation (Fig. 6.9) and again the performance of *Carex* is more noticeably affected by *Festuca* than the density, which suggests the two species are competing actively. Finally the relationship between *Festuca* and microtopography has a markedly negative correlation, as would be expected. The data were obtained from eight replicated lines of 10 cm quadrats, and the analyses accordingly show the mean dimension of scales of pattern. It is interesting to see how the co-variance analysis has picked out the level of interaction between the species concerned and the microtopography of the area, which enables the relative vigour of the species and also the relative effect of the environment (in this instance, microtopography) on the two species to be assessed.

7 The Causal Factors of Pattern

PATTERN in vegetation is the spatial arrangement of individuals of a species; correlation methods are usually employed to examine the detailed relationships existing between different species, but clearly both are different aspects of a general phenomenon. It is impossible to discuss one without considerations involving the other and, accordingly, the causal factors relating to pattern overlap, to a considerable extent, those factors relating to correlation discussed in Chapter 5. This separation of 'pattern' and 'correlation' is artificial, but has been made for the sake of clarity.

Since the initial demonstration by Gleason (1920) and Svedberg (1922) of patchy distribution of individuals in an apparently uniform area, a considerable effort has been made to detect non-randomness in vegetation. Most authors concluded that vegetative spread and heavy seeds were the two most likely factors which cause such an aggregation of individuals. Ashby (1948) endorsed these views but pointed out that 'overdispersion is present in species where there is no obvious biological reason for it'. He suggested that an overdispersed species may produce a secondary overdispersion among other species of the community, and this could possibly account for the otherwise inexplicable pattern (discounting obvious soil heterogeneity). Goodall (1952) and Greig-Smith (1952) both suggested that cyclical regeneration in patches as postulated by Watt (1947*a*) could produce pattern in vegetation, but there still remained numerous cases where an explanation was difficult. Following the development of techniques of pattern analysis (Greig-Smith 1952, 1961; Kershaw 1957, 1960), it is apparent that a very wide range of pattern scales are present in vegetation. Some of these patterns probably reflect a correspondingly wide range of variation of some factors of the environment. Sometimes it has proved impossible to understand all the factors responsible for a certain pattern and often a scale of pattern is related to one of the more obvious or more easily measured of a group of closely inter-related environmental factors.

1. MORPHOLOGICAL PATTERN

Where a species has a densely tussocked form, or where the basal leaves form a rosette, then the smallest pattern present in an analysis will be a measure of the mean size of an individual. In these cases it is clear that the morphology of a species will produce small scale pattern and, furthermore, this scale of pattern will be imposed on other species present. An example of apparent spatial exclusion is given by Kershaw (1958) for *Agrostis tenuis*, which showed a marked scale of pattern at 3.2 m. *Dactylis glomerata* and *Lolium perenne* also showed this same scale of pattern but were negatively associated with *Agrostis*, and thus appeared to be spatially excluded. In fact the distribution of these species was controlled in the area mainly by the depth of soil, *Agrostis* growing more densely on the shallower areas of soil, and the other species on the areas of deeper soil. Thus pattern which would appear at first sight to be due to spatial exclusion of one species by another, may in fact be controlled by independent factors of the environment.

Where the species under consideration has an extensive rhizome system, several scales of pattern are usually evident as the result of the characteristic system of branching and leaf-production of that species. Phillips (1954a) showed for *Eriophorum angustifolium* three scales of pattern that could be attributed to morphology (Fig. 7.1). The morphology of *Eriophorum* gives a characteristic grouping of aerial shoots (Fig. 7.2)

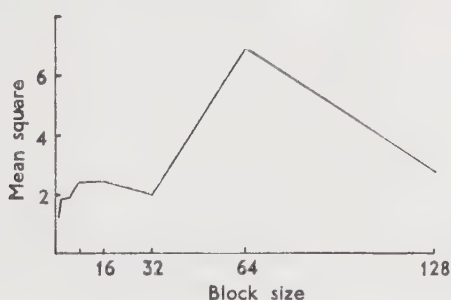


Fig. 7.1. Three scales of pattern in *Eriophorum angustifolium* represented by three peaks in the graph mean square/block size. (From Phillips 1954; courtesy of J. Ecol.)

separated by a length of rhizome which is equivalent to a year's increment of growth. The double primary peak is due to the grouping of shoots round the parent shoot from backwardly directed short rhizomes giving a peak at block size 2 (200 sq. cm) and a larger scale of grouping due to longer rhizomes directed forwards and giving a peak at block size 8 (mean

area 800 sq. cm). The large peak at block size 64 reflects the mean size of a complete individual (mean area 0.64 sq. m). A similar pattern series was detected in *Trifolium repens* (Kershaw 1959) with three scales of pattern

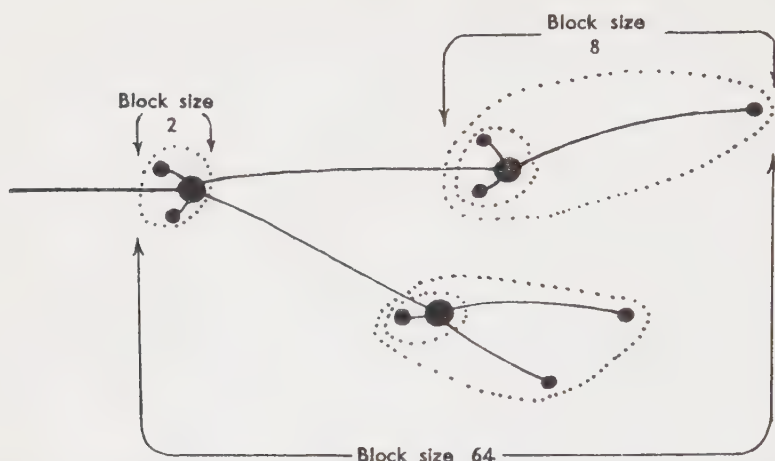


Fig. 7.2. Diagrammatic representation of the three scales of morphological pattern in *Eriophorum angustifolium*.

(Fig. 7.3) equivalent to first and second order branches and to the complete stolon system of the plant (Fig. 7.4). Numerous other examples of morphological pattern have been described (Agnew 1961; Anderson 1961*a*, 1961*b*; Greig-Smith 1961*a*, 1961*b*; Kershaw 1958, 1959; Kershaw and Tallis 1958), and in general, scales of pattern at small block sizes may be attributed to the morphology of the species.

The pattern due to the morphology of the rhizome can give useful information as to the level of performance of a species in different areas. It is clear that a measure of performance such as the mean annual extension of a rhizome system gives a good indication of the vigour of a plant and one which would be markedly controlled by the environment. Thus a series of pattern analyses from different plots over the range of distribution of a species should show a progressive shift of peaks which would reflect the changing morphology. Phillips (1954) demonstrated such a variation of morphology in *Eriophorum* growing in different plant communities; the scales of pattern reflecting the morphology of the rhizome were very much smaller where the habitat was less favourable. (Fig. 7.5 and compare Fig. 7.1 above.) Anderson (1961) and Kershaw (1959) discuss similar effects in *Vaccinium*, *Calluna*, *Pteridium* and *Trifolium* and it is apparent that valuable information can be obtained from comparisons of this sort.

The analysis of morphological pattern can also be related to the age of a rhizome system, as the pattern and size of branches vary with age and correspondingly alter the trend in a series of pattern analyses. The mor-

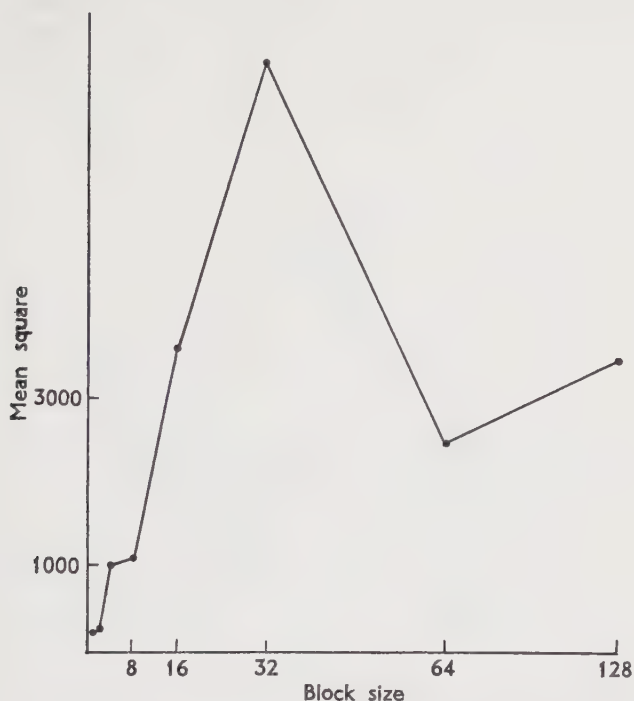


Fig. 7.3. Three scales of pattern in *Trifolium repens* shown by three peaks, at block size 1, 4 and 32, on the graph mean square/block size.

phological pattern of *Agrostis tenuis* colonizing a derelict sand pit shows such a progressive change (Kershaw 1958). The patches of sampled *Agrostis* varied in diameter from young clumps a few centimetres in diameter to large circular patches. The scales of pattern detected corresponding to the diameter of the patch are given below (Table 7.1). The three scales of pattern (block sizes 2, 8 and 32, equivalent to 2, 8 and 32 sq. in.) in the smallest clump correspond to first order branch and second order branch and to the complete rhizome system respectively. As the clumps increase in diameter the size of the complete rhizome system progressively increases, but the primary and secondary scales are simultaneously maintained. At the largest clump size investigated the maximum scale of pattern and the smaller scales of pattern are maintained and there appears a fourth scale of pattern which is caused by the primary branch systems separating away from the parent rhizome by decay of the

older parts and appearing as established individuals. These 'fragments' will presumably then follow the same cycle of events.

Thus the morphological pattern, though usually expected at the smaller block sizes, is of considerable interest and can be often helpfully used to demonstrate the relationship between the morphology of the individuals and the environment, or conversely a progressive change in morphology with time. It should be pointed out that not all small-scale patterns are necessarily morphological patterns, and in fact pattern at block sizes 1-2

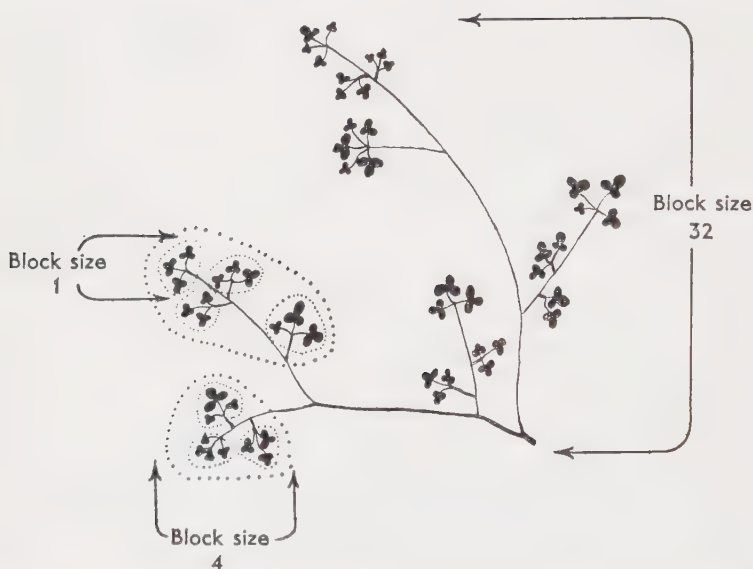


Fig. 7.4. Diagrammatic representation of the three scales of morphological pattern in *Trifolium repens*.

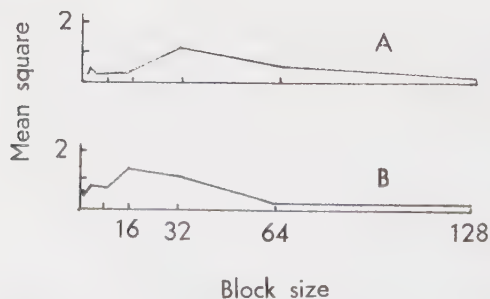


Fig. 7.5. The variation of pattern scales of *Eriophorum angustifolium* in two communities, *Calluna vulgaris*, *Erica cinerea* (A) and *Trichophorum caespitosum* (B). (From Phillips 1954; courtesy of *J. Ecol.*)

Table 7.1—The scales of pattern present in analyses of tiller density from clumps of *Agrostis* of varying diameter. (From Kershaw 1958; courtesy of J. Ecol.)

Clump width (inches)	Density of tillers	Peaks (square inches)			
38	1.26	2	8	32	
42	1.42	2	8		64
45	1.56	2	8		64
51	1.74	2	8		128
54	1.72	2	8-16		128
90	1.90	1	8	32	128

(mean dimensions 5–10 cm) has in several instances been attributed to other intrinsic properties of the plant, or of the community or environment (see below).

Chadwick (1960) describes an interesting historically determined pattern in *Nardus stricta*, which is best described as a large-scale morphological pattern. Two scales of pattern are detected, one at block size 2–4 (10–20 cm) caused by the morphology of *Nardus*, and a secondary peak at block size 32 (160 cm). The consistency of the secondary peak (Fig. 7.6) is surprising, and it would seem it is therefore not correlated with an environmental factor which would in fact fluctuate from site to site. Chadwick interprets this scale of pattern as the size of 'clone', reflecting the changes of rhizome growth since the grazing management of the Welsh mountains was changed. Thus with the advent of rationing in the first world war and the demand for smaller joints of meat the hill farmers changed over from old wethers which had effectively controlled the spread of *Nardus* by grazing, to breeding ewes which are much more selective in their grazing and do not touch *Nardus* unless more palatable species are absent. In response to this change the *Nardus* was able to spread and has actively done so ever since. Examination of the rhizome morphology shows a multidirectional growth, the old rhizome dying away behind and giving rise to a number of separate clumps each of which continues (as an individual) the centrifugal growth of the colony. The annual increment of growth is about 2 cm which over a period of 40 years would result in a scale of pattern of diameter of 160 cm equivalent in fact to the pattern at block size 32.

2. ENVIRONMENTAL PATTERN

The effects of major discontinuities of the environment on vegetation are usually well marked and, though such reactions of the vegetation result in patterns in the true sense of the word, these major effects, often on a large scale, are obvious as a change of floristic composition. Such a pattern

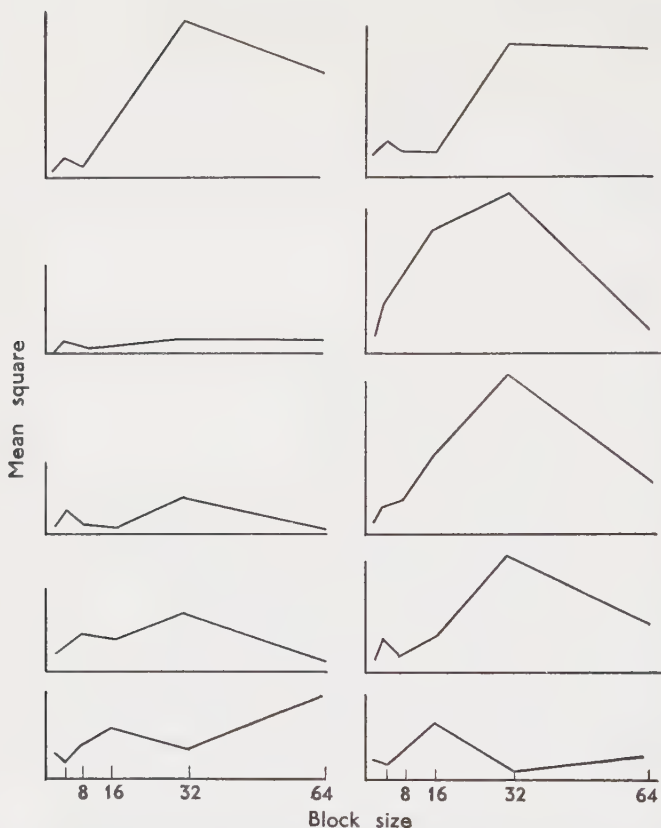


Fig. 7.6. The pattern scales of *Nardus stricta* in a number of upland grassland sites (see text). (From Chadwick 1960; courtesy of Blackwell Sci. Pub.)

is readily visible without recourse to quantitative method and calls for little comment. It has become increasingly evident that extremely small variations of an environmental factor (or factors) operating over quite large areas will produce a corresponding variation in the vegetation. Such patterns usually become apparent at the medium and larger block sizes in any particular area. Thus environmental pattern is developed in vegetation in response to a general and overall variation of one of the major environmental factors and produces a pattern of density distribution. The first demonstration of environmentally determined pattern showed the close relationship between the pattern of *Agrostis tenuis* and soil depth in an upland grassland area which was mentioned above (Kershaw 1958). The associated species *Dactylis*, *Lolium* and *Trifolium* were more abundant on the deeper areas of soil while conversely *Agrostis* was more dense on the

shallower soil and their pattern, though on the same scale, was in fact an inverse pattern. The mean rooting depths of these species under normal conditions suggests a possible explanation of this pattern: *Agrostis* normally produces a shallow root system whilst the other species root at much greater depths. Thus the limitation of root development in *Dactylis*, etc., seriously affects the capabilities of these species and accordingly they are only likely to survive on the areas of deeper soil (Kershaw 1959). The effect of a small variation in soil depth on the distribution of species in the area was initially somewhat unexpected, but it now seems highly likely that numerous other soil factors will be shown to have a measurable effect on the distribution of species within an area which at first sight appears to be uniform vegetation. Thus Anderson (1961a, 1961b) obtained a close correlation between the pattern of *Pteridium* and *Vaccinium* with the pattern of oxygen-diffusion rates. Greig-Smith (1961b) showed that the pattern of soil level formed of alternating hollows and mounds was correlated with the distribution of several dune slack species. Similarly, Kershaw (1962c) obtained a relationship between the micro-topography of a *Rhacomitrium* heath in Central Iceland and the distribution of *Carex bigelowii* and *Festuca rubra* (see above). In some reported investigations there is a marked pattern at the largest block size caused by an almost imperceptible slope in the area sampled and such a large and intense scale of pattern may often obscure smaller patterns due to other causes (see Greig-Smith 1961a). Similar, but more obvious, patterns have been reported by Billings and Mooney (1959), Billings and Mark (1961) and Warren Wilson (1952).

Pattern related to obvious surface micro-topographical variation will be controlled by the interaction of several environmental factors, which are in turn all closely related to topography. Thus it seems likely that drainage, availability of water, leaching, nutrient supply and pH would tend to vary together with changes in micro-topography and it would be difficult, if not impossible, to decide which factor or group of factors was directly controlling the distribution of a species. However, it is suggested that a slight fluctuation of pH or ion concentration would result in a detectable vegetational pattern, and it is interesting that Pigott has demonstrated considerable pH gradients over very short distances in the Burren Peninsula in Ireland. Snaydon (1962) has shown a similar steep pH gradient and also a gradient of calcium phosphate and potassium concentration, varying by a factor of up to 3 in a distance of only 2 ft (60 cm). It seems possible that similar or even steeper gradients will prove to be a general characteristic of undisturbed soils, producing the corresponding variations in the vegetation (see also Chapter 5). The critical demonstration and measurement of such micro-gradients and their corresponding effects on pattern is very slow and tedious and awaits the development of

instruments capable of rapid and accurate measurement of such soil factors in the field.

3. SOCIOLOGICAL PATTERN

The term 'sociological pattern' covers a range of pattern units which are the products of several inter-related causal factors operating at small block sizes (up to a pattern scale of 80 cm dimensions in grassland, for example). These factors are partly due to intrinsic properties of the plants themselves and partly due to the micro-environment. Thus sociological pattern is a product of the interaction of species on species and individual on individual which may or may not be directly modified by micro-environment.

These small-scale sociological effects often take the form of a mosaic of patches of different density levels dynamically related to each other in time and space. The causal factors of sociological pattern are not only dependent on the competitive ability of an individual (which may also be, in part, dependent on the micro-environment), but also on the possible presence of toxins exuded by an individual, and its age. Several of these relationships can be examined by correlation methods and have been discussed previously (Chapter 5). However, they are usually evident in studies of pattern and are included here for completeness.

Almost every effect of one species on another (excluding parasitism) is in the form of a modification of the environment and it is possible that the environmental pattern which limits the distribution (in terms of density) of a species was in the first place imposed on the environment by another species. Zinke (1962) investigated the modification of the environment under *Sequoia gigantea*, *Pinus contorta* and other species. These modifications were expressed by pH, nitrogen content and exchangeable bases in the surface mineral soil. There was a marked radial relationship between these soil factors and tree cover (Fig. 7.7) and it is readily understood how such a pattern of environmental factors would impose a corresponding pattern of ground vegetation detectable for several years after the removal of the tree cover. The steady accumulation of leaf litter and corresponding increase in soil nitrogen is a well marked and expected result of tree establishment in a given site. It is very likely that similar less obvious gradients are developed in relation to all perennial species and a mosaic of micro-environmental variations will be rapidly developed which will subsequently influence the establishment of other species or individuals in the area. Accordingly some small-scale patterns, which strictly speaking should be grouped under 'Environmental Pattern', may be included in this section. This is quite justified by the realization that under different conditions of the environment the outcome of competition may be different:

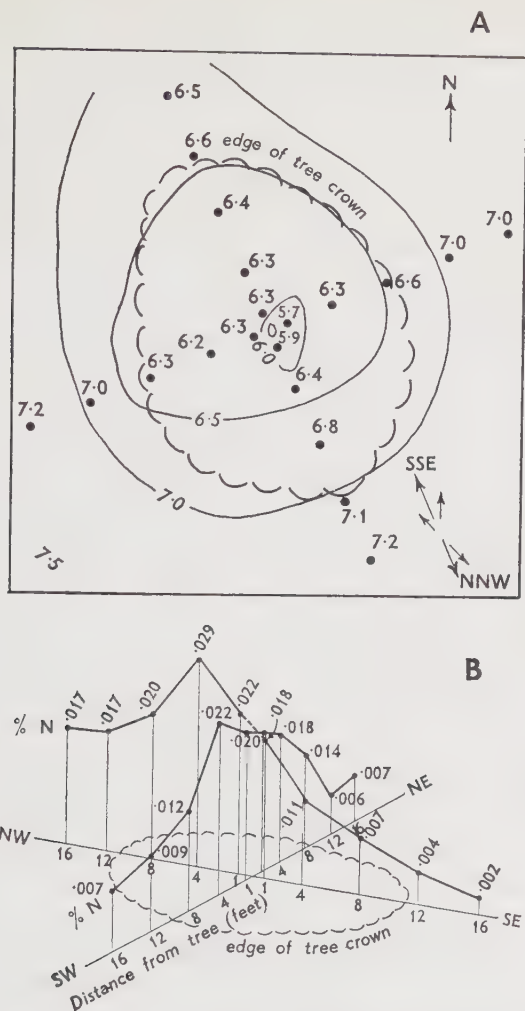


Fig. 7.7. The gradient of pH (*A*) and nitrogen (per cent by weight) (*B*) of surface mineral soil under a tree of *Pinus contorta*. The relative proportions of wind directions in the area are indicated. (From Zinke 1962; courtesy of *Ecology*.)

thus under a deficiency of soil nitrogen species *A* may suppress species *B* in competition although *B* could have grown satisfactorily in the absence of *A*; at a high level of soil nitrogen *B* may well be able to grow with *A* or even suppress it.

Since Watt (1947*a*) outlined several systems in which species were related in cyclical phasic development (see Chapter 4, p. 63), such cyclic phases have been suggested as one of the possible causes of pattern in

vegetation. Relatively few further examples of cycles involving several species have been reported in the literature and it would appear that such cycles are rather exceptional and therefore one has to look elsewhere for a general explanation of patterns which are not causally related to environment and morphology. On the other hand the description of cyclical *density* phases of *Pteridium* in a pioneer, building, mature and degenerate series (Watt 1947a, 1947b) (pp. 67–69), where the performance fluctuates, has been confirmed by several workers since (Chapter 4). This is distinct from cycles in which the actual species change in a recognizable sequence. Watt (1955) shows that *Calluna* follows the same phasic development and furthermore that *Pteridium* as an associated species is inversely related in its distribution to *Calluna*. Thus where *Calluna* is at its building/mature phases, bracken is at its minimum development; conversely where *Calluna* is in its degenerate phase bracken is very much more in evidence. Concurrently, the competitive ability changes with the age series described as pioneer, building, mature and degenerate.

The phasic development of *Pteridium* and *Calluna* have been confirmed by Anderson (1961a, and 1961b), Nicholson and Robertson (1958) and the 'marginal effect' or 'advancing front' as described by Watt (1947) and representing the pioneer and building phases, has also been reported in several additional species. Thus Ovington (1953), Caldwell (1957) Penzes (1959, 1960) and Kershaw (1962a) have described many examples of advancing fronts of even-aged rhizomes at an optimum level of performance (p. 70). Quantitative data showing the relationship between performance and age in *Alchemilla alpina* and *Carex bigelowii* (Kershaw 1960b, 1962c) (Figs. 4.12, p. 73 and 4.14, p. 74) together with the general observations on the occurrence of advancing fronts, suggests that the performance of most if not all perennial plants will vary with age. Correspondingly the variation of competitive ability with age (Watt 1955) is likely to be a general phenomenon. Data on the variation of density of *Salix herbacea* as it is invaded by an 'advancing front' of *Eriophorum angustifolium* are given by Kershaw (1962) and confirm the relationship between age and competitive ability. The variation in density of *Salix* taken from a line of contiguous quadrats running through a circular patch of *Eriophorum* actively invading a *Salix herbacea* sward has been discussed previously (p. 71) and the data show the density of *Salix* to be negatively related to the density of *Eriophorum* (Fig. 4.9, p. 71). Furthermore the performance of *Eriophorum* (leaf length) is negatively related to the density of *Salix*. Thus when *Eriophorum* is at an optimum level of performance and density, the density of *Salix* is at a minimum. Since performance varies with age, and the ability to compete varies with the general level of performance of an individual, most if not all perennial plants will have gradually diminishing competitive ability with increase in age. Age as a

causal factor of pattern would appear to be of considerable and widespread importance in perennial species, and a mosaic of *density phases* of a species imposed by the varying competitive ability of an associated species is of frequent occurrence and quite independent of any other environmental consideration.

A similar pattern effect has been described by Cooper (1960, 1961) who suggests that pattern in ponderosa pine stands results from cyclical development governed by fire. As an old-aged stand degenerates young trees invade and establish, rapidly forming an even-aged group. Such groupings are maintained by the inability of young pines to establish underneath mature parents, and also by periodic fires which remove any young small scattered saplings that do occur. An even-aged stand once established remains as a single unit until the degeneration phase is reached. An area of pine thus consists of a mosaic of phases at different density levels, each group being of a different age.

Sociological pattern is also caused by the effect of an individual on the environment which can be quite independent of the age factor of the individual. The reaction produces a modification of the environment which reduces or enhances the chance of survival of progeny either of the same species or of other species merely, for example, by the annual deposition of leaf litter (see p. 122, Zinke 1962). The interpretation of such instances is by no means as clear cut as would be imagined. The dependence on shrub cover for some herb species can be interpreted as a response to the accumulation of leaf litter or shelter, or protection from grazing, or protection from grass competition, etc., but considerable argument has developed around this phenomenon as to the likelihood of the direct inhibition of associated species by certain shrub species. The case of *Encelia farinosa* is capable of two apparently reasonable interpretations. The lack of ground vegetation under the shrub may be a reflection of toxic substances in its leaves but it may equally reflect the failure of this shrub to accumulate beneath it a fine soil tilth. Other species which contain equally powerful toxins in their leaves and yet can accumulate leaf litter and good soil tilth may also have a dense associated ground flora. The existence in the field of a chemical substance actively exuded by plant roots in quantities sufficiently great to control the establishment or development of associated species, has yet to be demonstrated (see also p. 86), but the possibility of such control of one species by another seems sufficiently probable to necessitate its inclusion in any consideration of pattern.

A very puzzling feature of some rhizomatous species has been reported by Kershaw (1958, 1962) where the aggregation of aerial shoots, arising from different and separate rhizome systems as small 'clumps' 5-10 cm in diameter, is responsible for what at first sight would be regarded as merely a very small-scale morphological pattern.

A typical arrangement of rhizomes and tillers is given below (Figs. 7.8 and 7.9) for an area of both recently established and mature *Calamagrostis*

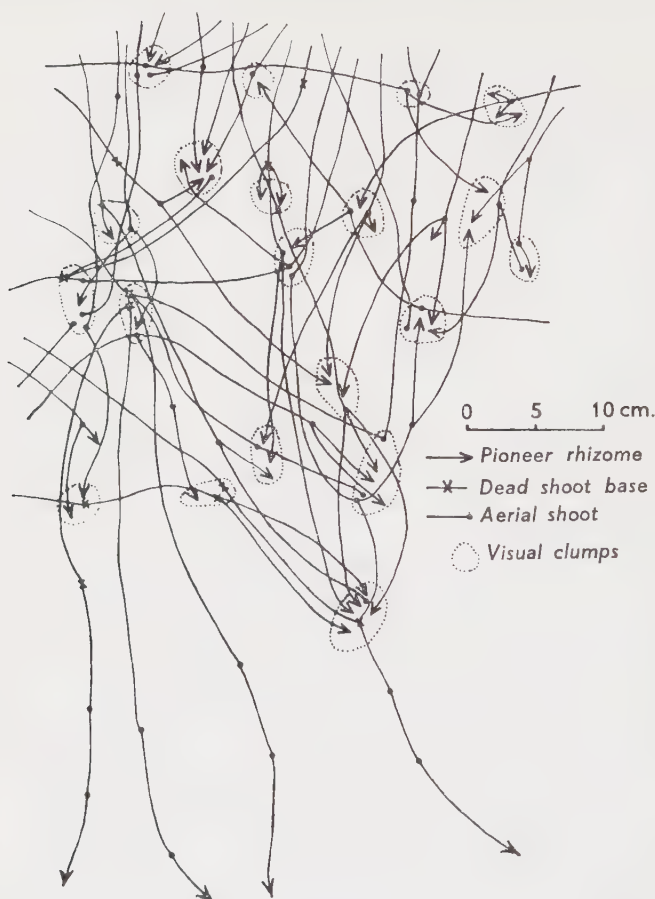


Fig. 7.8. The arrangement of aerial shoots and rhizomes of *Calamagrostis neglecta* invading bare mud. (From Kershaw 1962; courtesy of *J. Ecol.*)

neglecta in central Iceland (Kershaw 1962). The pattern is quite marked, the small clumps being composed of at least three, and often four or five different rhizome systems. It has been suggested that the consistent orientation of rhizomes and the production of tillers in the form of a clump, may be related to micro-gradients of some environmental factor as yet undetermined, down which the rhizomes grow; finally, tillering occurs at a point where the factor responsible is at its maximum level. However, the possibility does exist that a more orderly and positive mechanism exists.

It could be due to the chemical stimulation of a rhizome apex by an established aerial shoot and accordingly this type of pattern is included

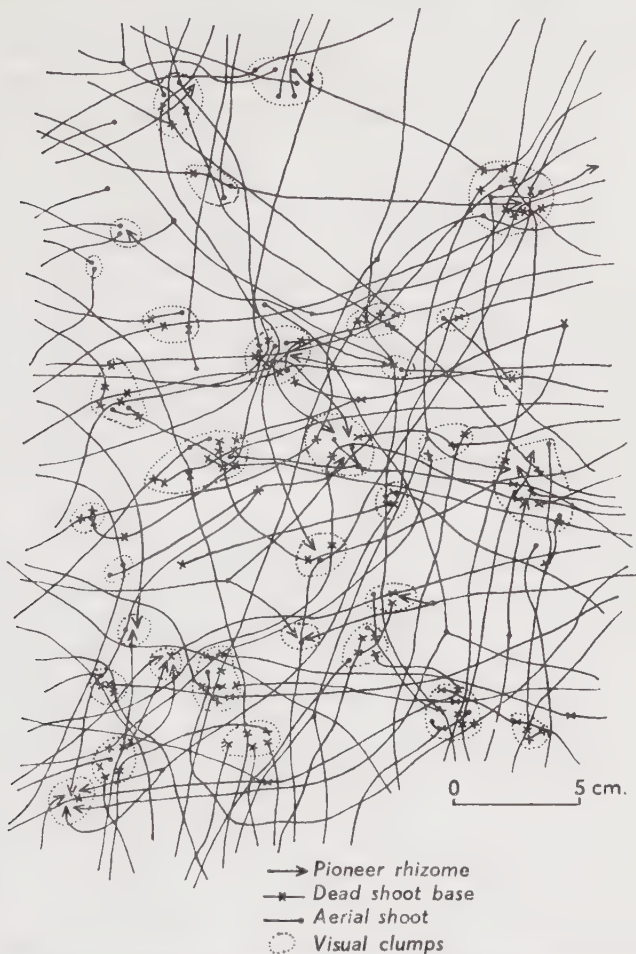


Fig. 7.9. The arrangement of aerial shoots and rhizomes in an established sward of *Calamagrostis neglecta* in Iceland. (From Kershaw 1962; courtesy of J. Ecol.)

temporarily at least as a sociological pattern. Whatever the mechanism, it should be emphasized that small-scale pattern should not be immediately dismissed as morphological pattern.

Contagious distribution of individuals (clumping) in vegetation is a common feature, yet little evidence has appeared to suggest that regular distribution of individuals (underdispersion) is of more than rare occurrence in vegetation. The most likely situation which would produce regular distribution is one where there is a high density of individuals within

a uniform area; the resulting active competition would limit both the total density over the area, and at the same time the spatial distribution of an individual relative to its neighbours. The lack of data demonstrating regular distribution suggests that either the theoretical conditions leading to competition between individuals for environmental factors are rarely fulfilled, *or are over-shadowed by extreme variations of environmental factors which are able to impose a marked pattern on the species as a whole*. Thus it should be emphasized that even though there is marked contagion at one particular block size, at a similar or larger block size there may be an indication of regular distribution of individuals or of pattern units. As Greig-Smith (1952a) states, 'Professor Bartlett (personal communication) has made a preliminary examination of the problem and his provisional conclusions may be briefly summarized as follows: (1) Variance may be expected to rise to a maximum value as block size reaches the *mean area of clump*, diminishing thereafter if the clumps are underdispersed. . . .' Thus if there is a sharp fall of variance following a marked peak, it can be assumed that the units of pattern have a regular distribution in the area examined.

It is important, however, to bear in mind that such a regular distribution of pattern units is relative to the size of the area investigated, and it is almost certain that an increase in size of the sampling area would show the existence of higher scales of pattern. The evidence to date suggests that frequently there occurs a regular distribution of pattern units up to a limited scale beyond which a further scale of contagion appears. Thus regular distributions of individuals or groups of individuals, rather than being completely absent, are over-shadowed by the scales of contagion present.

In general it is difficult to categorize causalities which are included here under 'sociological' factors for it is virtually impossible to discriminate in the field between effects due to competition and effects due to micro-variations of the environment. The demonstration of positive or negative association between species is straightforward, but determination of competition between species very often necessitates experimentation (see Chapter 3). In certain instances some indication can be obtained from field data: thus Kershaw (1959) showed in *Dactylis* and *Lolium* a sociological scale of pattern at 80 cm. His decision was based on a significant negative association at high densities and nil association or even a slight positive association at low densities. This change of trend in association with increasing density does suggest competition rather than effects of slightly dissimilar environmental requirements.

A similar example is given by Vasilevich (1961) for *Cladonia sylvatica* and *C. rangiferina* in the ground vegetation of pine forest in Russia. The two species are positively associated at low densities and negatively at high

densities, again suggesting competition between the species at high densities. A further example of sociological pattern which shows negative association between species which is, in part at least, related to competition is taken from the relationship between *Carex bigelowii* and *Festuca rubra* (Kershaw 1962c) (p. 111). Both the density and performance data of *Carex* are positively related to micro-topography and negatively related to the density of *Festuca*. However, the performance of *Carex* is more markedly affected by *Festuca* than is the density of *Carex*, which again suggests an effect of competition. (See also Fig. 6.9, p. 112.)

GENERAL CONSIDERATIONS

The widespread detection of non-randomness in vegetation, usually in the form of contagion or clustering of individuals, has led to the realization that all vegetation will contain one or many scales of pattern. The only possible exception to this is in the colonization of a homogenous bare area when the initial migrules may be distributed more or less at random. Morphological scales of pattern will always be present, and it is rare to find an area with such a completely uniform environment as not to produce one or more scales of environmental pattern. The presence of pattern in environmentally uniform areas is also to be expected since intrinsic properties of the plants themselves will interact to produce pattern. Thus it is difficult to envisage an area where all the individuals are of an even age and hence have equal levels of performance and competitive ability. Accordingly we are forced to the conclusion that pattern will always be present in vegetation except in a few rare and extreme cases.

8 The Detection of Natural Groupings of Species

THE two opposing schools of thought who on the one hand consider the climax association to be a complex organism or quasi-organism and on the other hand those who support the individualistic concept, also reflect the present-day ecological approaches to the delimitation and definition of community units. Thus the concept of the complex organism implies considerable interaction between the species which jointly modify the environment and form a distinguishable vegetational group. Conversely the individualistic concept regards no two communities as being identical, but considers that they show a continuous variation and accordingly can not be readily delimited as definable units. Numerous attempts have been made in recent years to extract statistically or objectively definable units from vegetation, by means which range from complex statistical procedures to rather simple subjective methods. There is a considerable amount of controversy and since the position has changed markedly in the past few years only the more widespread approaches will be considered in any detail.

THE BRAUN-BLANQUET SCHOOL OF PLANT SOCIOLOGY

The aim of the Braun-Blanquet school (Braun-Blanquet 1932, 1951) is a world wide classification of plant communities based on a number of concepts which have recently been critically reviewed by Poore (1955, 1956). The initial attitude of the British ecologists to these methods and to the results was one of extreme criticism, but more recently attempts have been made to understand more fully what the Continental workers are attempting to achieve and the vegetation of the Scottish Highlands has been comprehensively treated by McVean and Ratcliffe (1962) on this basis.

The foundation of the classificatory system is the *association* which is the basic vegetational unit and is an abstraction obtained from a number of lists of species from selected sites in the field.

Table 8.1 gives an association table for the *Rhacomitrium*/*Carex bigelowii* association made up of twelve lists based on the Domin scale with

details of each stand incorporated at the head of the table. From such an association table it is possible to pick out those species which occur in a given number of stands, i.e. the *degree of presence* can be assessed for all species. Braun-Blanquet expresses the degree of presence of a species in a five-degree scale:

- 5 = constantly present (in 80–100 per cent of the stands).
- 4 = mostly present (in 60–80 per cent of the stands).
- 3 = often present (in 40–60 per cent of the stands).
- 2 = seldom present (in 20–40 per cent of the stands).
- 1 = rare (in 1–20 per cent of the stands).

Thus in the *Rhacomitrium/Carex* association table (Table 8.1) *Carex bigelowii*, *Dicranum fuscescens*, *Polytrichum alpinum*, *Rhacomitrium lanuginosum*, *Cetraria islandica* and *Cladonia uncialis* occur with a degree of presence 5; similarly *Vaccinium myrtillus* and *Festuca vivipara* have a degree of presence 4, and so on down to such species as *Lycopodium selago*, *Nardia scalaris*, *Coriscium viride*, with a degree of presence 1. Where the data of species presence is derived from samples taken from plots of known and limited area the degree of presence is referred to as the *degree of constancy*.

CONSTANCY

It is clear that if a very large sample area is used many more species will be 'constant'; this leads to a discussion of the minimal area concept which will be postponed to a later section (see below). The method of obtaining the lists and measures used have been described fully in Chapter 1, but several further concepts are of considerable and fundamental importance.

CHOICE OF SITE

The association tables are derived from a large number of *carefully chosen sites* and it is clear that the whole basis of the system is established on a markedly non-random sampling procedure. The first important proviso in the choice of a sample plot is its homogeneity. Dahl and Hadač (1949) define homogeneity in the following way:

A plant species is said to be homogeneously distributed in a certain area if the possibility to catch an individual of a plant species within the test area of given size is the same in all parts of the area. A plant community is said to be homogeneous if the individuals of the plant species which we use for the characterization of the community are homogeneously distributed.

Table 8.1—*Rhacomitrium*/*Carex bigelowii* association table. (From Poore 1955; courtesy of J. Ecol.)

No. of sample plot	520010	520011	520035	520064	520068	520076	520117	520162	520167	520144	520006	520193
<i>Empetrum hermaphroditum</i>	2	—	—	—	4	1	—	—	—	—	—	—
<i>Salix herbacea</i>	—	—	—	—	—	—	3	—	—	—	—	—
<i>Vaccinium myrtillus</i>	5	3	—	—	4	3	3	3	3	4	4	—
<i>V. vitis-idaea</i>	—	1	—	—	2	2	2	—	1	—	—	—
<i>Lycopodium selago</i>	3	—	—	—	—	2	—	—	—	—	—	—
<i>Agrostis canina</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>A. tenuis</i>	1	3	3	—	2	3	—	—	—	—	—	—
<i>Deschampsia flexuosa</i>	5	—	—	—	—	—	3	—	—	—	—	—
<i>Festuca ovina</i> agg.	3	—	—	—	—	—	—	—	—	—	—	—
<i>F. vivipara</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>Nardus stricta</i>	1	—	—	3	3	4	2	3	1	2	2	1
<i>Carex bigelowii</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>Luzula multiflora</i>	4	4	4	4	3	3	3	5	4	4	6	9
<i>L. spicata</i>	—	—	—	—	—	—	—	—	1	—	—	—
<i>Alchemilla alpina</i>	—	—	—	—	—	1	2	—	—	—	—	—
<i>Galium hercynicum</i>	1	—	—	—	—	3	1	—	—	—	2	—
<i>Dicranum fuscescens</i>	1	1	2	—	—	2	2	—	—	—	2	1
<i>D. scoparium</i>	—	1	2	2	2	—	3	1	4	3	3	3
<i>Aligotrichum hercynicum</i>	1	1	—	—	—	—	1	2	—	—	—	—
<i>Pleurozium schreberi</i>	—	3	—	—	—	1	1	—	—	—	—	—
<i>Pohlia?</i> <i>annotina</i>	—	—	—	—	—	1	—	—	—	—	4	—
<i>Polytrichum alpinum</i>	3	—	1	—	—	—	—	—	—	—	—	—
<i>Rhacomitrium lanuginosum</i>	9	—	10	3	2	2	3	3	1	3	3	2
<i>Rhytidadelphus loreus</i>	—	7	10	10	9	9	10	10	10	10	6	9
? <i>Aplozia sphaerocarpa</i>	1	—	1	—	—	—	—	—	—	—	1	—
<i>Diplophyllum albicans</i>	1	—	—	—	1	1	—	—	—	—	—	—

Nardia scalaris	-	-	-	-	-	-	I	-	-	-
Lophozia? ventricosa	-	-	-	-	-	-	I	-	-	-
Ptilidium ciliare	-	-	-	-	-	-	-	-	-	-
Alectoria nigricans	-	-	-	-	-	I	-	-	-	-
Cerania vermicularis	-	I	I	I	2	-	2	2	2	-
Cetraria aculeata	-	-	-	-	I	-	I	3	2	-
Cetraria islandica	2	I	2	3	2	I	I	2	2	3
Gladonia alpicola	-	-	2	-	I	-	-	-	-	-
C. bellidiflora	I	-	-	I	I	-	I	I	-	-
C. coccofera	-	-	-	I	I	-	-	-	-	-
C. crispata	-	-	-	-	I	I	-	-	-	-
C. furcata	-	-	-	-	I	-	-	-	-	-
C. gracilis	-	-	-	-	I	-	2	I	2	-
C. pyxidata	I	-	-	-	-	I	-	-	-	-
C. rangiferina	-	-	-	-	-	-	-	-	-	-
C. sylvatica	-	-	-	-	-	2	3	2	2	I
C. squamosa	-	I	I	I	-	-	-	I	-	-
C. uncialis	4	3	3	2	3	I	3	3	3	I
Coriscium viride	-	I	-	-	-	I	-	-	-	-
Icnadophila sp.	-	-	-	-	-	-	-	I	-	-
Ochrolechia frigida	-	-	-	I	-	I	-	2	-	-
Sphaerophorus globosus	-	-	-	-	-	2	-	I	-	-

The accumulated evidence relating to the species distribution patterns present in all vegetation types so far examined (Chapter 7), throws considerable doubt on the existence of the homogeneous plot ideally suitable for formulation of the association table. Dahl and Hadač recognize the difficulty and state:

In nature plant communities are never fully homogeneous, i.e. the density of the species of importance by the characterization of the community, especially the dominating species, have not exactly the same density in all parts of the area. We may thus talk of more or less homogeneous plant communities. Measurements on the homogeneity of the plant community are rarely carried out, but the human eye, badly adapted to measurement but well to comparison, rapidly gives the trained sociologist an impression whether a plant community he has before his eyes is highly homogeneous or not.

Again this seems extremely doubtful since a large number of patterns have been detected in areas which appeared absolutely uniform even to the most careful inspection. This aspect of the method has also been severely criticized by Goodall (1954) who states '... and it is pointed out that no area of vegetation has ever been shown to be fully homogeneous. It is even doubted whether areas with greater and smaller variance between replicate samples may be distinguished in natural vegetation.'

MINIMAL AREA AND HOMOGENEITY

Assuming there is a reasonable degree of uniformity the second proviso is that the stand must be sufficiently large to enable a representative sample to be taken. This minimum size requirement of the sample is termed the *minimal area* and is related to the number of species which occur as the sample plot increases in size. With a small plot the number of species present is also small but as the size of the plot is increased the number of species increases very noticeably. Eventually the number of new species found in successively larger plots becomes progressively fewer. This general trend is apparent in a graph of the number of species against the area of the sample plot, or a species area curve as it is usually called. The Braun-Blanquet concept of minimal area is related to the area at which the species-area curve becomes approximately horizontal. A number of examples of species-area curves are given below (Fig. 8.1) all broadly similar and of characteristic form. It is apparent that though the slope of the curve changes fairly markedly there is a continued increase in the number of species as the area of the sample plot is further enlarged. Hopkins (1957) presents a clear account of the use of species-area curves relative to the determination of minimal area (see also Goodall 1952,

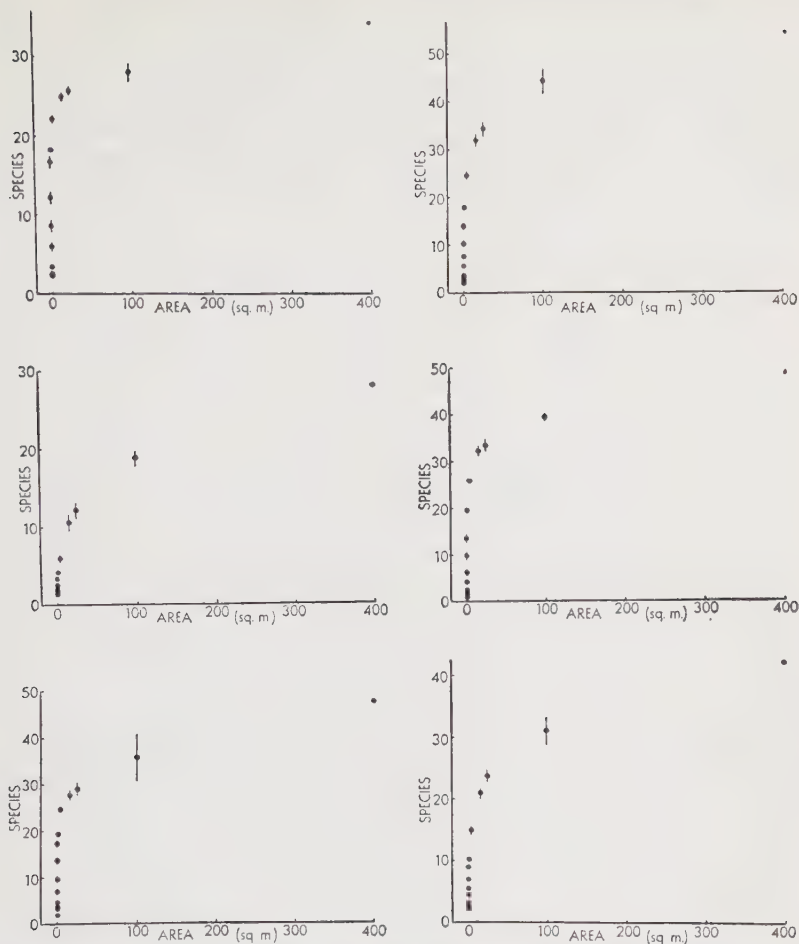


Fig. 8.1. Species area curves from six sample sites. (From Hopkins 1957; courtesy of *J. Ecol.*)

Greig-Smith 1957) and draws attention to the extreme difficulty of establishing any certain definition of the minimal area. Thus the concept of minimal area depends on a definite 'break' in the curve. Cain (1932, 1934) claimed that such a break could be 'recognized' but later (1938) pointed out that its position depended on the ratio of the axes used. Following this a number of attempts to determine the minimal area based on the ratios of species and area have been made. A similar approach was made by DuRietz (1921) who related the number of constant species to area in constancy-area curves, 'constants' being defined as species which have a percentage frequency greater than 90 per cent and the minimal area de-

defined as 'the smallest area on which an association attains a definite number of constants'. Hopkins (1955) gives a number of constancy-area curves (Fig. 8.2) of a very similar form to the species-area curves and with the same attendant difficulty in determining the position of the minimal area. He concludes: 'Thus minimal area cannot be determined objectively from the species-area or constancy-area curve.'

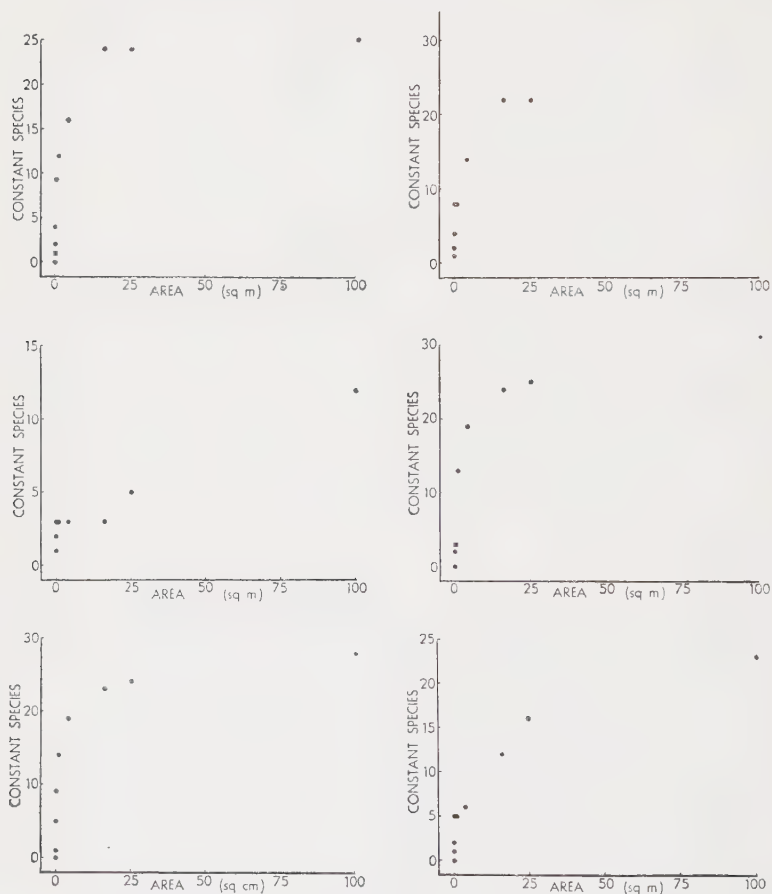


Fig. 8.2. Constancy-area curves from six sample sites (From Hopkins 1957; courtesy of *J. Ecol.*)

The problems of homogeneity and minimal area outlined above are inter-related. If true homogeneity existed then minimal area would be a valid concept. However it is clear from the existence of pattern at numerous scales in apparently homogenous vegetation that minimal area can never be more than a gross approximation and accordingly some subjective

judgement is necessary in assessing whether the area sampled is large enough to reflect the characteristics of that particular community.

A more recent review of the Braun-Blanquet system by Moore (1962) avoids the problems of homogeneity and minimal area by accepting the subjectivity of the approach and suggesting that a long 'tail' of isolated occurrences at the foot of an association table is a sign of a badly chosen stand. The fact that this does occur is clear evidence of the impossibility of visually assessing homogeneity and the minimal area required for sampling even by an experienced worker.

THE ASSOCIATION

The mechanical construction of the association table has been described above and the subsequent steps are a careful examination of the tables and separation of any lists which differ consistently and noticeably from the rest. These differences vary considerably from minor variations to more obvious differences which may necessitate the establishment of another association. Poore (1955) sums up this stage of the procedure as 'muddled and haphazard'. 'According to Braun-Blanquet these decisions can only be made by having recourse to a consideration of the fidelity of the various species, and this stage (that of distinguishing associations by faithful species) is one about which the literature is particularly reticent. Apart from the proviso that it requires much time and experience we are told nothing, and observation of the system in use has done nothing to unravel the problem for me.' This seems to be a fair comment on the abstraction of the associations that have been established. Fidelity is a characteristic of certain species which shows a degree of exclusiveness towards a particular association. Thus Braun-Blanquet (1952) lists five degrees of fidelity.

FIDELITY 5. Exclusive species, completely or almost completely confined to one community.

FIDELITY 4. Selective species, found most frequently in a certain community but also rarely, in other communities.

FIDELITY 3. Preferential species, present in several communities more or less abundantly but predominantly in one certain community and there with a greater degree of vigour.

FIDELITY 2. Indifferent species, without a definite affinity for any particular community.

FIDELITY 1. Accidentals, species that are rare and accidental intruders from another community or relics of a preceding community.

Poore is correct in saying the only situation in which degrees of fidelity can be properly assessed is that which exists when all the vegetation of a region has been described. He quite rightly lays emphasis on 'constancy'

to delimit the association groupings rather than determining the association by the species faithful to them (fidelity grades 3-5). The difference between 'constancy' and 'fidelity' may not at first sight be clear but would seem to be related to the ecological tolerance of the species. Thus a 'constant' species may have a wide ecological tolerance and occur in several associations, while a species with a high degree of 'fidelity' has a narrow ecological tolerance and only occurs in one association. The situation is rendered even more confusing by an example quoted by Poore (1955a) taken from Barkman (1940). The example is an epiphytic association and the association table comprises fourteen lists with seven faithful species. Of the fourteen lists, one contains 5 of the faithful species, one 3, two 2, eight 1, and two 0. Poore expresses his difficulty in deciding which criteria were adopted in retaining the majority of these lists in this association. It would appear that either the associations are based in fact on constancy, in which case degree of fidelity seems unnecessary, or the sites are chosen because species of known narrow ecological amplitude are present, and these species subsequently, by circular argument, are defined as the faithful species. Thus faithful species are those which are confined to one association and the association is recognized by these faithful species; this is perfectly legitimate if the association is delimited by other characteristics in the first place. If in fact the association is recognized by its faithful species it is then not valid to define the faithful species from the associations. Moore (1962) denies the over importance of fidelity and quotes Braun-Blanquet (1959): 'It should not be concluded, as has sometimes been maintained, that the associations are based on fidelity. This is emphatically not the case. The association is an abstraction based on the totality of more or less homogeneous relevés (lists) which floristically correspond closely to one another. It is however, characterized, not merely floristically but also ecologically, dynamically and geographically. Nevertheless, in distinguishing from one another the associations which have been conceived on a floristic basis, far greater importance and more general significance is attributed to fidelity than to purely quantitative characteristics especially when fidelity is combined with high constancy.' This latter instance would seem to be of importance and considerable value, but as has been pointed out only possible when the complete vegetation of a region has been described. Accordingly Poore's approach based on constancy seems fully justified.

However, it is still a subjective decision to separate out a number of lists from an association table which have one or two species in common and set up a further association. There seems to be no objective reason why the splitting should stop there. Moore (1962) attempts to elucidate this point but states: 'In order to understand this (how the association under discussion is arrived at), it is essential to grasp the principle of the differential

species.' It is this tendency for emphasis of fidelity and the suspicion of a circular argument which so reduces the value of the approach. Poore's insistence on the use of the 'constant' species to delimit the 'association' is a great improvement but subjective decisions still have to be taken as to the 'level' of the association and whether a certain group of lists legitimately represent a fragment of a further association. Poore (1956) used a method of successive approximation; if no obvious constants were present in the lists they were taken together and divided on probable differential species (species consistently present in one group of lists). Provisional constants were named and sites were sought which possessed these combinations of constants. If the constants were real such stands were readily found but if not, they proved impossible to find.

Braun-Blanquet, having established a number of associations then classifies them into a hierarchy, which is a convenient if an unnatural system. The shortcomings of the continental system are rather numerous and have been discussed above under each step of the procedure. The modifications as proposed by Poore (1955, 1956) to a large extent remove some of the major criticisms and a workable system is available for the rapid description and characterization of a large area of vegetation. However, the sampling procedure, i.e. the choice of a sample site, is entirely subjective, and the apparent sharpness of the limits of associations are in fact a result of this non-random method of sampling. The sites which are clearly intermediate are avoided as 'not homogenous' and as large numbers of intermediates exist, even if they occur rarely, the sociological approach involving avoidance of such sites over-simplifies the picture to a considerable extent. This by no means invalidates the real existence of the associations that have been erected and they are obviously of frequent and widespread occurrence. A more real interpretation of the association should be based not only on its floristic composition but also on its frequency of occurrence in a region. The term 'noda' introduced by Poore is a satisfactory one and does imply the existence of intermediates of less frequent occurrence relative to the 'central type'. The difficulty of finding an area which is homogenous and of accurately defining the minimal area relative to it is unavoidable. It is worthwhile to accept these limitations within the system outlined by Poore, since it can readily contribute considerably to our knowledge of the vegetation especially in those regions where we have little or no floristic information at all.

CORRELATION METHODS

The subjective nature of the delimitation of vegetational units as proposed by the Continental and Scandinavian sociologists have led to numerous attempts at establishing similar units by objective methods. The

basic method so far employed is to calculate the expected number of joint occurrences of species in pairs and compare this with the observed value by means of a χ^2 test. The methods used differ both in the way the final data is presented as well as in the details of the sorting of the data.

Two classificatory arrangements have been used, multi-dimensional and hierarchical. The former utilizes the concept of multiple inter-relationships between vegetational groupings and represents the classification as a dimensional network. The actual location of the species in the diagram is controlled by positive associations detected between pairs of species. The distance between two associated species is usually directly related to the degree of association between them.

On the other hand a hierarchical system positions a number of species characterizing specific species groupings in descending order of importance, again the degree of association being used to determine the relative position of each species. This presents a tidy and organized classification but one which is highly artificial and has little ecological meaning. The method undoubtedly arose as a result of the parallel hierarchical classification used in taxonomy with the implied phylogeny and genetical relationships between the different groups. However, in ecology no such relationship exists and a hierarchical classification may well separate two groups of plants which prefer acid conditions since one grows in a wet bog and the other in a dry heath. This is well summarized by Webb (1954), and though such a classification appears to be readily assimilated and orderly it is an erroneous and over-simplified version of the real state of affairs.

DIMENSIONAL SPECIES RELATIONSHIPS

The variation of floristic composition of communities dominated by *Juncus effusus* in North Wales was examined by Agnew (1961). He examined 99 stands chosen at random from a potentially large number of areas where *Juncus* occurred. The presence or absence of each species was recorded in each site. Species which occurred less than five times in the total samples were eliminated and 2×2 contingency tables constructed for the remaining 53 species. The correlations obtained (Fig. 8.3) were diagrammatically represented in the form of a two-dimensional spatial arrangement of species (Fig. 8.4).

The reciprocal of the calculated value of χ^2 between each species pair is used to construct the diagram. Thus two species highly positively associated and with a large χ^2 -value are positioned close to one another. In practice some approximation is necessary since a three-dimensional arrangement of species is being condensed into two dimensions. The arrangement of species reflects positive correlations in the main, the

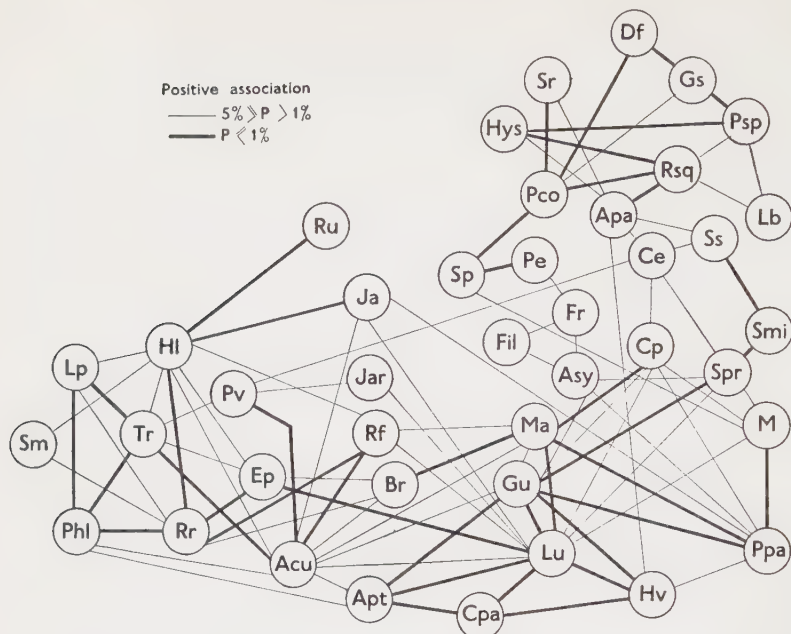


Fig. 8.4. The species 'constellation' based on chi-square values and showing positive correlations from 99 *Juncus effusus* stands. (From Agnew 1961; courtesy of *J. Ecol.*)

Acu *Acrocladium cuspidatum*
 Apa *Aulacomnium palustre*
 Apt *Achillea ptarmica*
 Asy *Angelica sylvestris*
 Br. *Brachythecium rutabulum*
 Ce *Carex echinata*
 Cp *Carex panicea*
 Cpa *Cirsium palustre*
 Df *Deschampsia flexuosa*
 Ep *Epilobium palustre*
 Fil *Filipendula ulmaria*
 Fr *Festuca rubra*
 Gs *Galium saxatile*
 Gu *Galium uliginosum*
 Hl *Holcus lanatus*
 Hv *Hydrocotyle vulgaris*
 Hys *Hylocomium splendens*
 Ja *Juncus acutiflorus*
 Jar *Juncus articulatus*
 Lb *Lophocolea bidentata*
 Lp *Lolium perenne*

Lu *Lotus uliginosus*
 M *Molinia caerulea*
 Ma *Mentha aquatica*
 Pco *Polytrichum commune*
 Pe *Potentilla erecta*
 Phl *Phleum pratense*
 Ppa *Potentilla palustre*
 Psp *Pseudoscleropodium purum*
 Pv *Prunella vulgaris*
 Rf *Ranunculus flammula*
 Rr *Ranunculus repens*
 Rsq *Rhytidiadelphus squarrosus*
 Ru *Rumex acetosa*
 Sm *Stellaria media*
 Smi *Scutellaria minor*
 Sp *Sphagnum palustre*
 Spr *Succisa pratense*
 Sr *Sphagnum recurvum*
 Ss *Sphagnum subsecundum*
 Tr *Trifolium repens*

general position of each group of species being related to the negative correlations also present. On pure chance alone some correlations will be significant (1 in 20 at a 5 per cent significance level) and accordingly those species with only a single correlation at a 5 per cent level are not included

in the diagram. It is immediately obvious that three groupings of species occur (see Fig. 8.4).

GROUP 1 (left-hand side of the diagram)

Holcus lanatus, *Lolium perenne*, *Phleum pratense*, *Ranunculus repens*, *Stellaria media* and *Trifolium repens*.

GROUP 2 (lower right-hand side of the diagram)

Angelica sylvestris, *Carex panicea*, *Galium uliginosum*, *Hydrocotyle vulgaris*, *Lotus uliginosus*, *Molinia coerulea*, *Potentilla palustris* and *Succisa pratensis*.

GROUP 3 (upper right-hand side of the diagram)

Aulacomnium palustre, *Deschampsia flexuosa*, *Hylocomium splendens*, *Polytrichum commune*, *Pseudoscleropodium purum*, *Rhytidiadelphus squarrosus* and *Sphagnum recurvum*.

It is equally clear that none of the three groupings are isolated and distinct entities, each is linked to the adjacent group by correlations between member species of the respective groups or through an intermediate species, e.g. *Juncus acutiflorus*. Agnew suggests it is possible that such intermediate species may prove on a more extensive survey to be part of additional groupings. The deduction that these correlated groupings of species represent significant 'communities' or plant associations (in the sense intended by Braun-Blanquet) is considerably strengthened by additional ecological information. Thus the general linear relationship of the three groups follows a pH gradient which is highly significant ($r = -0.509$, $p < 0.001$).

Welch (1960) presents a similar series taken from woodland in Tanganyika (Fig. 8.5). The very obvious grouping on the left of the diagram represents a group of species which form dense thickets, the central group linked to the thicket species through *Albizia*, *Canthium* and *Acacia pennata* represents a group of pioneer species which invades abandoned cultivated land. Similarly the group of species on the right of the diagram represent a woodland association dominant in some adjacent areas. The three groups in fact reflect the initial and secondary stages of two lines of succession. DeVries (1953) examined a large number of grassland sites in Holland and estimated the percentage frequency of the species in each of the sample sites. Correlation coefficients were calculated and the data presented in the form of a two-dimensional diagram (Fig. 8.6) based on positive correlations similar to the *Juncus effusus* example above. Again a number of groupings are present, all of them inter-related yet forming fairly distinct ecological groupings.

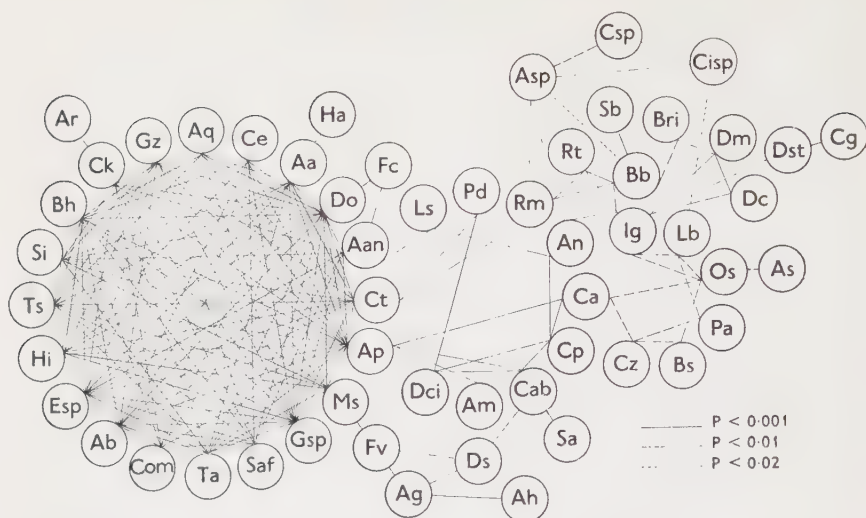


Fig. 8.5. Positive associations between plant species in woodland in Tanganyika.
(From Welch 1960; courtesy of *J. Ecol.*)

Aa	<i>Allophylus alnifolius</i>	Dci	<i>Dalbeya cincinnata</i>
Aan	<i>Albizia anthelmintica</i>	Dm	<i>Dalbergia melanoxydon</i>
Ab	<i>Albizia brachycalyx</i>	Do	<i>Dalbergia ochracea</i>
Ag	<i>Acacia gerrardii</i>	Ds	<i>Dombeya shupangae</i>
Ah	<i>Albizia harueyi</i>	Dst	<i>Dalbergia stuhlmannii</i>
Am	<i>Acacia mellifera</i>	Esp	<i>Euphorbia</i> spp
An	<i>Acacia nigrescens</i>	Fc	<i>Fagara chalybea</i>
Ap	<i>Acacia pennata</i>	Fv	<i>Flueggea virosa</i>
Aq	<i>Azela quanzensis</i>	Gsp	<i>Grewia</i> spp
Ar	<i>Asparagus racemosus</i>	Gz	<i>Gelonium zanzibarense</i>
As	<i>Acacia senegal</i>	Ha	<i>Harrisonia abyssinica</i>
Asp	<i>Acacia</i> sp	Hi	<i>Haplocoelum inopleum</i>
Bb	<i>Brachystegia boehmii</i>	Ig	<i>Isoberlinia globiflora</i>
Bh	<i>Brachylaena hutchinsii</i>	Lb	<i>Lonchocarpus bussei</i>
Bn	<i>Bridelia niedenzii</i>	Ls	<i>Lannea stuhlmannii</i>
Bs	<i>Boscia salicifolia</i>	Ms	<i>Mamilkara sulcata</i>
Ca	<i>Combretum apiculatum</i>	Os	<i>Ostryoderris stuhlmannii</i>
Cab	<i>Cassia abbreviata</i>	Pa	<i>Pterocarpus angolensis</i>
Ce	<i>Carissa edulis</i>	Pd	<i>Phyllanthus discoideus</i>
Cg	<i>Combretum ghasalense</i>	Rm	<i>Royena macrocalyx</i>
Cisp	<i>Cissus</i> sp	Rt	<i>Randia taylorii</i>
Ck	<i>Capparis kirkii</i>	Sa	<i>Steganotaenia araliacea</i>
Com	<i>Commiphora</i> spp	Saf	<i>Spirostachys africana</i>
Cp	<i>Commiphora pilosa</i>	Sb	<i>Sclerocarya birrea</i>
Csp	<i>Cordia</i> sp	Si	<i>Strychnos innocua</i>
Ct	<i>Canthium telidosma</i>	Ta	<i>Thylachium africanum</i>
Cz	<i>Combretum zeyheri</i>	Ts	<i>Teclea simplicifolia</i>
Dc	<i>Dichrostachys cinerea</i>		

This method of approach has several advantages, the initial subjective choice of site is eliminated to a large extent and a partial-random choice can be made at least. The initial decision of the type of site (a grassland woodland, *Juncus* community) is obviously unavoidable. Secondly the groupings of species are completely objective and present a more realistic picture with the inter-relationships and almost continuous variation of the groupings readily appreciated. At the same time the element of constancy is present and Agnew (1961) suggests *Trifolium repens*, *Potentilla palustris* and *Galium saxatile* represent constants for groups 1, 2 and 3 respectively. Also the artificial hierarchical classification is avoided and if a sufficiently widespread survey was made, the *dimensional* interrelationships of a large number of associations could be readily defined. The major disadvantage of the approach lies in the lengthy computation necessary where the number of sites is large. Since the larger the number of samples the more complete and significant the inter-relationships become this is a serious disadvantage. However the recent availability of computers invalidates such a criticism and it is obvious that this approach will prove to be of considerable value in the future.

HIERARCHICAL SYSTEMS BASED ON CONTINGENCY TABLES

The initial contribution to this method was made by Goodall (1953). It is of considerable interest and will accordingly be described in some detail. Again 2×2 contingency tables were prepared from presence and absence data of all species in a *Eucalyptus oleosa*/*E. dumosa* association in Australia. The area was topographically uneven with sandy ridges running east and west separated by hollows with a heavier soil. An area 640 m square was delimited and divided into 64 square plots within each of which four 5 m quadrats were placed at random. Fifty-eight species were recorded from the area but 27 only occurred in less than 5 quadrats and were eliminated. χ^2 values were calculated for the occurrence of the remaining species in pairs. Only positive associations (in the sense that the species were positively correlated) were used in the classification of the quadrat data. Goodall points out that homogenous groups of quadrats can be obtained (which is the object of a system of classification) by eliminating correlation between species in either of four ways.

(a) Quadrats with one of two species which are correlated can be separated out as an initial potentially homogeneous group.

(b) Quadrats not containing one of the species represent a similar potentially homogeneous group.

(c) Quadrats containing both the species.

(d) Quadrats containing neither of the species.

GROUP 1 (top left of the diagram)

Molinia caerulea, *Sieglingia decumbens*, *Carex panicea*, *Potentilla erecta* and *Cirsium dissectum* typical of acidic soils of low fertility.

GROUP 2 (bottom left of the diagram)

Glyceria maxima, *Caltha palustris*, *Phalaris arundinacea*, *Lychnis flos-cuculi*, *Carex disticha*, *Ranunculus repens*, *Glyceria fluitans* and *Alopecurus geniculatus*, typical of moist neutral-acidic grassland.

GROUP 3 (top right of the diagram)

Arrhenatherum elatius, *Trisetum flavescens*, *Dactylis glomerata*, typical of dry hay meadows.

GROUP 4 (bottom right of the diagram)

Lolium perenne, *Cynosurus cristatus*, *Poa pratense*, *Agrostis stolonifera*, *Plantago major* and *Trifolium repens*, typical of fertile neutral pastures.

Goodall analysed the data by the four methods and found reasonable agreement in the results, and concluded that the first system, the presence of a pair of correlated species, was the most convenient method of approach.

The first step was to separate out from the total sample (256) those quadrats containing *Eucalyptus dumosa* which showed a number of highly significant correlations with other species,* and was the most frequently occurring species in the area (170 quadrats). Within this group of quadrats several highly significant positive correlations were still present and a second division was made, again on the most frequent species, *Triodia irritans*, which showed a highly positive correlation with some other species. One hundred and nineteen quadrats were separated out and again fresh contingency tables established and the heterogeneity of these 119 quadrats examined. The process was continued with successively smaller groups of quadrats until finally 53 quadrats selected on the presence of *Eucalyptus dumosa*, *Triodia irritans* and *Stipa variabilis* showed no significant correlation between species within the group and were finalized as a homogenous group (group A). All the remaining quadrats (203 in all) were pooled and a fresh series of contingency tables constructed. The same procedure was followed and the most frequent species *Eucalyptus oleosa*, in this residual group of quadrats was used as the initial division (121 quadrats). Subsequently 92 quadrats containing *Bassia*

* This in fact is 'association' between species that is measured but the term correlation is employed here to avoid confusion with the use of 'association' in the Braun-Blanquet methodology.

uniflora and finally 17 quadrats containing *Cassia eremophila* were separated out.

This final group of 17 quadrats showed no significant correlations and were established as group *B*. The remaining 186 quadrats were again examined by 2×2 contingency tables, divisions being based either on the most frequent species which showed significant correlation or on the next

Table 8.2—Frequency (per cent) of species in four groups of quadrats based on presence of single species showing positive correlations. (From Goodall 1953; courtesy of *Austr. J. Bot.*)

Frequencies of 50 per cent or more have been given in bold type

Species	Group			
	<i>A+E</i>	<i>B</i>	<i>C</i>	<i>D</i>
	Number of quadrats			
	83	17	66	90
<i>Acacia rigens</i> A. Cunn.	2	0	5	0
<i>Bassia parviflora</i> Anders	2	0	0	4
<i>B. uniflora</i> R. Br.	17	100	5	100
<i>Beyeria opaca</i> F. Muell.	1	6	5	0
<i>Callitris verrucosa</i> R. Br.	1	0	26	0
<i>Cassia eremophila</i> A. Cunn.	1	100	0	2
<i>Chenopodium pseudomicrophyllum</i> (1)	5	6	2	22
<i>C. pseudomicrophyllum</i> (2)	12	6	0	13
<i>Danthonia semiannularis</i> R. Br.	20	0	6	7
<i>Dodonaea bursariifolia</i> Behr.	53	0	71	17
<i>D. stenozyga</i> F. Muell.	1	0	0	6
<i>Enchylaena tomentosa</i> R. Br.	4	24	0	3
<i>Eucalyptus calycogona</i> Turcz.	14	18	11	30
<i>E. dumosa</i> A. Cunn.	81	12	100	39
<i>E. oleosa</i> F. Muell.	49	100	24	81
<i>Grevillea huegelii</i> Meiss	5	35	8	4
<i>Kochia pentatropis</i> R. Tate	2	24	0	7
<i>Lepidosperma viscidum</i> R. Br.	1	0	9	0
<i>Lomandra leucocelphala</i> R. Br.	4	0	8	0
<i>Melaleuca pubescens</i> Schau.	4	0	8	0
<i>M. ucinata</i> R. Br.	55	0	53	3
<i>Micromyrtus ciliatus</i> J. M. Black	0	0	9	0
<i>Myoporum platycarpum</i> R. Br.	2	0	5	0
<i>Olearia muelleri</i> Bth.	5	59	0	6
<i>Santalum murrayanum</i> F. Muell.	1	12	5	1
<i>Stipa elegantissima</i> Lab.	1	12	0	3
<i>S. mollis</i> R. Br.	7	0	5	10
<i>S. variabilis</i> Hughes	87	88	0	78
<i>Triodia irritans</i> R. Br.	78	6	100	3
<i>Vittadinia triloba</i> D.C.	46	24	11	37
<i>Westringia rigida</i> R. Br.	6	71	5	3
<i>Zygophyllum apiculatum</i> F. Muell.	4	65	2	47

most frequent species with a significant correlation. After the final separation of a homogenous group the total remaining quadrats were subsequently examined each time. The data was divided by this means into five homogenous groups assessed by χ^2 tests. Each group was finally re-combined with each of the other groups in turn and tested for heterogeneity. If the homogenous groups were satisfactory then recombination with other groups would immediately introduce correlation. This was found to be so, with the exception of groups *A* and *E* which on combination showed no significant correlations and were accordingly separated as

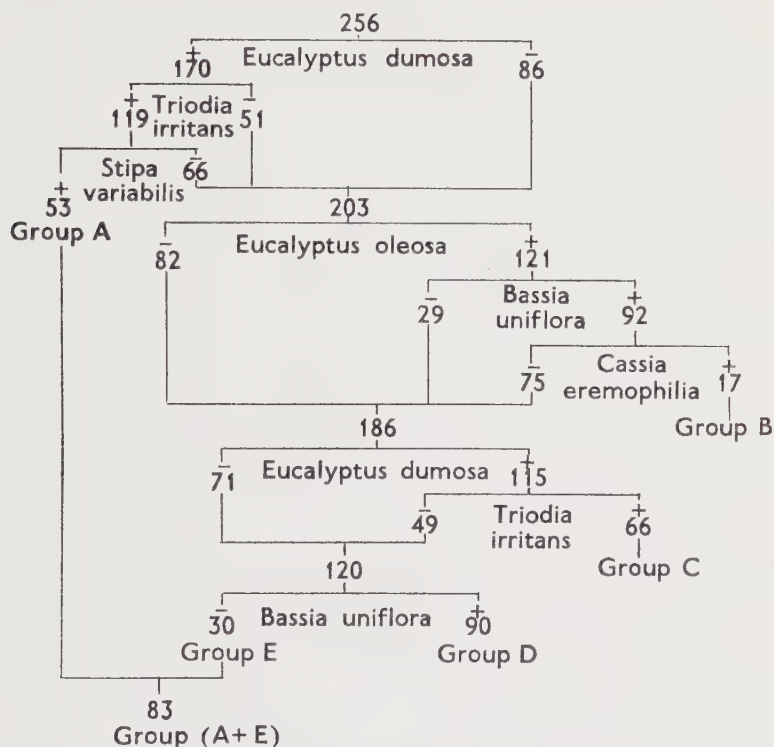


Fig. 8.7. Victoria Mallee vegetation. Stages in the classification of quadrats into groups. At each stage the number of quadrats in which the species in question is present (+) and absent (-) is indicated. (From Goodall 1953; courtesy of *Austr. J. Bot.*)

a single unit (Fig. 8.7). The species components of the groupings are given in Table 8.2. Goodall characterizes the four groups *A*, *B*, *C* and *D* by *Vittandinia triloba*, *Cassia eremophila*, *Dodonaea bursariifolia* and *Bassia uniflora* based on those species of most frequent occurrence in those

quadrats allotted to the same grouping by all four procedures. The distribution of the groupings in relation to the area studied (Fig. 8.8) shows

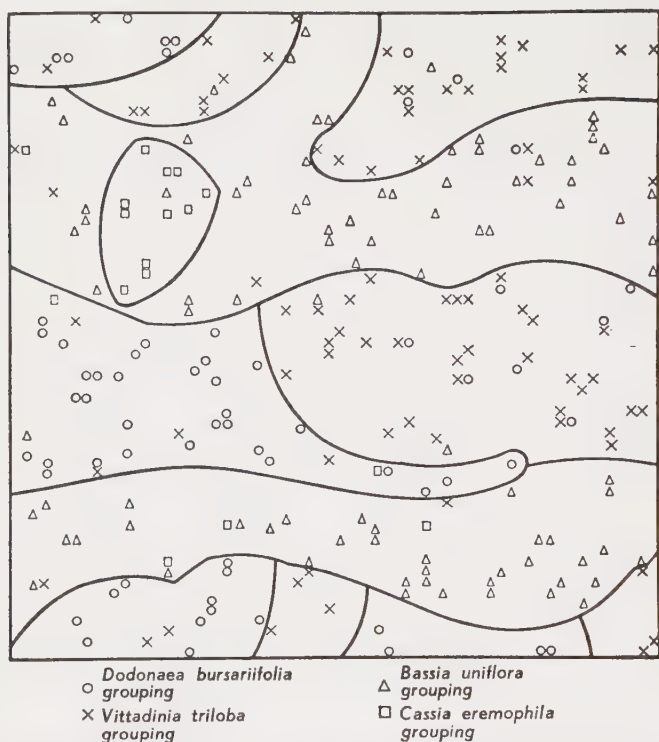


Fig. 8.8. Plan of the area of Mallee vegetation studies indicating the position of each quadrat and the grouping to which it was assigned. (From Goodall 1953; courtesy of *Austr. J. Bot.*)

a reasonable correlation with topography. Three ridges run across the area and are occupied predominantly by the *Dodonaea* and *Vittadinia* groupings while the hollows between contain the *Bassia* and *Cassia* groupings.

A similar approach leading to a hierarchical classification has been outlined by Williams and Lambert (1959, 1960). They have three main criticisms of Goodall's method: his use of positive correlations only, his use of the most frequent species as a basis of division of a potentially homogenous group, and the pooling of those quadrats which do not form the initial and successive homogenous groups. The use of negative correlations as well as positive ones greatly strengthens the analysis, as long as due regard is given to the size of quadrat used for sampling since

negative correlation between species may frequently occur by virtue of the fact that no two individuals can occupy the same place at any one time. Their criticism of the 'pooling' of quadrats seems equally logical: 'Imagine a population divided on species X into (X) and (x) . (X) is still found to be divisible on species Y into (XY) and (Xy) . Goodall would "pool" (Xy) with (x) to form a new population. Our chief objection to this system is that information relating to the discontinuity $(X)/(x)$ is being discarded,

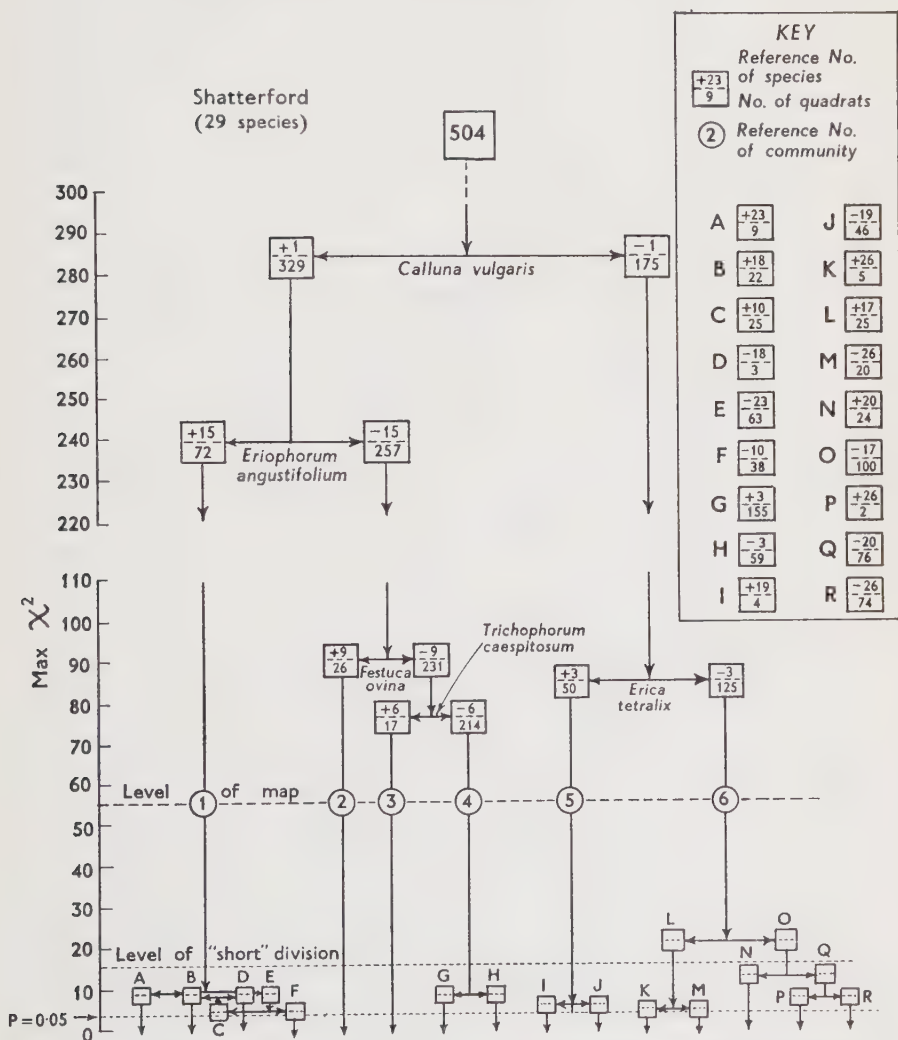


Fig. 8.9. The Shatterford community analysis. (From Williams and Lambert 1960; courtesy of *J. Ecol.*)

and on these grounds we would prefer a "hierarchical" system—a division, once made, would remain inviolate throughout the analysis.' It is also pointed out that Goodall's final groups are not necessarily capable of definition in terms of key species and also that the means by which the groups are obtained do not give any meaningful information.

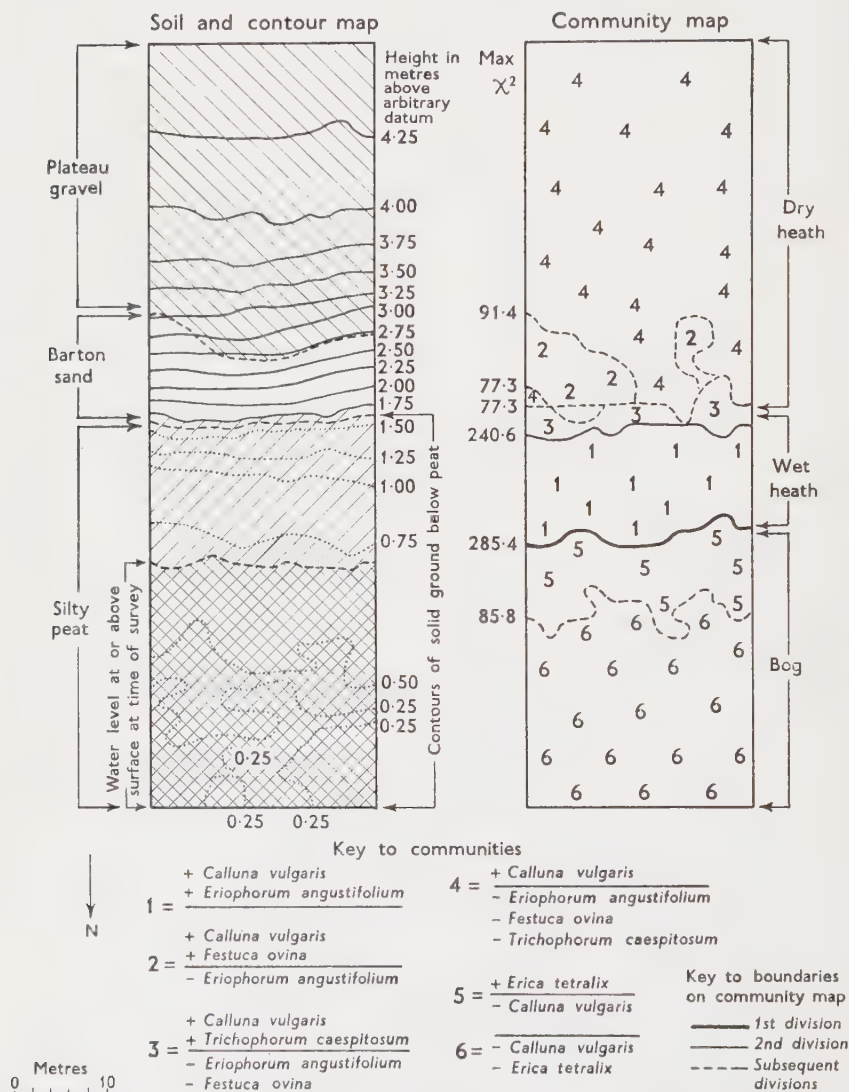


Fig. 8.10. The Shatterford community map, soil type, and contours. (From Williams and Lambert 1960; courtesy of *J. Ecol.*)

2×2 contingency tables are used to establish a χ^2 matrix and the χ^2 values are summed irrespective of whether they reflect a positive or a negative correlation. The species with the largest $S(\chi^2)$ and not the most abundant species is used in the sub-division of the sample, the two quadrat groups thus formed then remaining separate throughout the remainder of the sorting procedure. Each of the two groups is re-examined and further divided on the species with the largest $S(\chi^2)$. The hierarchical division is continued until no significant correlations appear, at which point the group is designated as 'final'. Williams and Lambert give several convincing examples of the application of the method to actual field data. The Shatterford example involving 29 species is extremely clear-cut, the analysis (Fig. 8.9) separating out six major groups which are further subdivided into a larger number of smaller units. The spatial distribution of the individual quadrats in relation to the soil variations of the area is remarkably consistent (Fig. 8.10). The first division (community 4) represents the area of dry heath dominated by *Calluna vulgaris* with *Erica tetralix* and *Molinia caerulea*. Communities 5 and 6 are typical bog communities dominated by *Erica tetralix* and *Molinia caerulea* respectively with community 1 occupying an intermediate 'wet heath' position (Table 8.3). From the species composition of the groupings and the relative frequency of occurrence the 'constant' species of the groupings are readily apparent. Thus the analysis appears to accomplish all that was intended for it and has the great advantage (in common with Goodall's approach) that the position of each group of quadrats can be accurately plotted on a map and related to the detailed environmental variations of the area as a whole. Thus any group of quadrats can be picked out at a later date and the environmental inter-relationships considered in detail.

Both methods however have certain drawbacks. The problem of computing large numbers of χ^2 values has been removed by the development of electronic computers in recent years and the initial limitations on the size of sample and number of species which could be handled in any one analysis have disappeared to a great extent. However, one serious difficulty lies in the relationship between quadrat size and the trend of correlation detected. This has been discussed in detail in Chapter 2 and Kershaw (1961) has shown that the final quadrat groupings depend largely on the size of the quadrat used. The Primary divisions are not likely to be affected by quadrat size but such overall differences are readily apparent on visual inspection of such an area, and do not need an elaborate technique to pick them out. On the other hand these methods are objective, and for the primary survey of an area very effective. The representation of the relationships is artificial and the delimitation of the groupings more clear cut than in fact they really are. In this context the dimensional representation of Agnew (1961), etc., is more satisfactory. However, from a

Table 8.3—Species composition of Shatterford groupings at six-community level. (From Williams and Lambert 1960; courtesy of *J. Ecol.*)

Ref. number of community	4	2	3	1	5	6
Number of quadrats	214	26	17	72	50	125
<i>Erica cinerea</i> L.	29	19	—	—	—	—
<i>Ulex minor</i> Roth	22	22	—	—	—	—
<i>Festuca ovina</i> L.	—	26	—	—	—	—
<i>Pinus sylvestris</i> L.	1	—	1	—	—	—
<i>Calluna vulgaris</i> (L.) Hull	214	26	17	72	—	—
<i>Polygala serpyllifolia</i> Hose	8	19	5	30	1	—
<i>Erica tetralix</i> L.	155	26	17	72	50	—
<i>Molinia caerulea</i> (L.) Moench	155	26	17	72	50	125
<i>Trichophorum caespitosum</i> (L.) Hartman	—	3	17	70	10	—
<i>Drosera rotundifolia</i> L.	—	—	7	58	23	4
<i>Juncus squarrosus</i> L.	—	—	—	5	—	—
<i>Gentiana pneumonanthe</i> L.	—	—	—	2	—	—
<i>Eriophorum angustifolium</i> Honck.	—	—	—	72	50	77
<i>Narthecium ossifragum</i> (L.) Huds.	—	—	—	57	49	25
<i>Drosera intermedia</i> Drev. and Heyne	—	—	—	9	15	—
<i>Carex panicea</i> L.	—	—	—	1	32	4
<i>Potentilla erecta</i> (L.) Rausch.	—	—	—	1	2	2
<i>Myrica gale</i> L.	—	—	—	4	47	76
<i>Juncus bulbosus</i> L.	—	—	—	—	1	2
<i>Carex rostrata</i> Stokes	—	—	—	—	1	8
<i>Juncus acutiflorus</i> Hoffm.	—	—	—	—	4	37
<i>Potamogeton polygonifolius</i> Pourr.	—	—	—	—	2	23
<i>Agrostis ? gigantea</i> Roth	—	—	—	—	1	20
<i>Carex echinata</i> Murr.	—	—	—	—	1	28
<i>Scutellaria minor</i> L.	—	—	—	—	—	26
<i>Cirsium dissectum</i> (L.) Hill	—	—	—	—	—	15
<i>Hypericum elodes</i> L.	—	—	—	—	—	3
<i>Potamogeton natans</i> L.	—	—	—	—	—	2
<i>Eleocharis pauciflora</i> (Lightf.) Link	—	—	—	—	—	1

classification point of view if classification is necessary, the resultant over simplification inherent in the χ^2 methods of analysis is probably beneficial in the first instance. Once knowledge has accumulated as to the composition of the 'central types' of associations, the intermediates can be subsequently included, completing the floristic description of a large area in detail.

THE CONTINUUM

The use of presence as a diagnostic feature is a utilization of only one of a number of characteristics which are available in describing a community. An important feature of a community is the abundance of the individual components relative to each other and relative to other communities. This aspect of community characterization and its use in classification of communities has been more widely used by the Curtis school in America which (like Gleason) holds the view that vegetation is a continuum and

cannot be classified into discrete entities (associations in the Braun-Blanquet sense). The development of the continuum approach was due to Cottam (1949) and Curtis and McIntosh (1950, 1951) and is one of the more important aspects of ecology in America.

The choice of sampling sites was made on criteria which avoids any preconceived ideas and eliminates as far as possible the non-random selection of sites inherent in Braun-Blanquet's method. Thus any woodland stand was sampled which was 'natural' (not planted), of adequate size (15 acres being the minimum) and not disturbed as far as could be determined by grazing, excessive cutting or fire. All the species of trees, herbs, shrubs were included and the frequency, density and dominance measured. Cottam (1949) defined frequency as the percentage occurrence of a species in the total sample (p. 16), density as the total number of individuals of a species relative to the total area examined, and 'dominance' is expressed as basal area. From the frequency, density and dominance values a 'relative importance' value was derived by addition of the values, the DFD index (Curtis 1947). Subsequently these measures were modified by Curtis and McIntosh (1950) and used in the form of:

$$\text{Relative density} = \frac{\text{Number of individuals of species}}{\text{Total number of individuals of all species}} \times 100$$

$$\text{Relative frequency} = \frac{\text{Frequency species} \times}{\text{Sum of frequency values of all species}} \times 100$$

and similarly relative dominance is used instead of dominance.

These measures are totalled and constitute the *importance value*, which can range from 0 to 300. The subsequent treatment of the data is most suitably described by reference to a specific set of data, given by Brown and Curtis (1952). The data relate to upland Conifer-hardwood forests of northern Wisconsin, the sampling sites being chosen by the criteria listed above with the additional feature of the absence of standing run-off water. For each stand in turn, an importance value is calculated for each species present and by inspection of the importance values each stand is assigned a *leading dominant*, i.e. that species with the highest importance value. Having designated the leading dominant in each stand, the data is then sub-divided so that each group of stands has the same leading dominant. Obviously some of the subordinate species in any one stand will be the leading dominants of other stands and consequently a fresh importance value is then calculated for each species based on the group of stands with their common leading dominant. In the conifer-hardwood data the leading dominants (Table 8.4) are *Tsuga canadensis*, *Quercus rubra*, *Betula lutea*, *Acer rubrum*, *Betula papyrifera*, *Pinus strobus*, *Populus tremuloides*, *Pinus resinosa*, *Quercus ellipsoidalis* and *Pinus banksiana* in decreasing

order of importance (importance values 25, 22, 21, 7, 6, 1, 1, 0, 0 and 0 respectively). *Acer rubrum* and *Betula lutea* do not achieve dominance in any stand and accordingly are not included by Brown and Curtis in the provisional arrangement of 'leading dominants'. These two species considered apart, the remaining mean importance value in those stands dominated by *Acer saccharum* give a general basis for the arrangement of the leading dominants in a phytosociological order. Thus *Pinus banksiana* has an importance value of 0 and is generally ecologically accepted as a typical pioneer species in Wisconsin, the remaining species falling between this and the final 'climax' association dominated by *Acer saccharum*.

Table 8.4—Average importance value of trees in stands with given species as leading dominant—104 stands. (From Brown and Curtis 1952; courtesy of *Ecol. Monog.*)

Number of Stand	Leading dominant	<i>Acer saccharum</i>	<i>Tsuga canadensis</i>	<i>Betula lutea</i>	<i>Acer rubrum</i>	<i>Quercus rubra</i>	<i>Betula papyrifera</i>	<i>Pinus strobus</i>	<i>Pinus resinosa</i>	<i>Populus tremuloides</i>	<i>Quercus ellipsoidalis</i>	<i>Pinus banksiana</i>
23	<i>Acer saccharum</i>	145	25	21	7	22	6	1	—	1	—	—
23	<i>Tsuga canadensis</i>	40	152	47	11	3	5	4	3	—	—	—
6	<i>Quercus rubra</i>	27	1	3	29	138	23	10	8	5	3	—
6	<i>Betula papyrifera</i>	48	8	7	27	16	108	19	1	29	1	—
19	<i>Pinus strobus</i>	12	6	2	24	12	12	150	39	9	5	—
9	<i>Pinus resinosa</i>	3	—	1	12	15	14	56	156	24	4	2
4	<i>Populus tremuloides</i>	11	—	—	10	29	34	14	19	140	—	—
4	<i>Quercus ellipsoidalis</i>	—	—	—	5	7	1	11	9	9	103	56
10	<i>Pinus banksiana</i>	—	—	—	3	3	3	13	12	14	36	213

The next highest importance value to *Acer saccharum* is *Tsuga canadensis* and accordingly this is placed in an adjacent position to *Acer saccharum*. Confirmation of the validity of this is obtained from the relative size of the mean importance value of the species in the *Tsuga* dominated group. Thus (discounting *Betula lutea*) *Acer saccharum* has the highest importance value and should thus be close to the group which is in fact dominated by *Acer saccharum*. On this basis and with due consideration to the columns of numbers both horizontal and vertical, approaching at least a smooth curve, the remaining leading dominants are arranged. On the basis of the

order of the leading dominants the remaining tree species are included, and an arbitrary climax adaptation number ranging from 1 to 10 is assigned to each species (Table 8.5). *Pinus banksiana* is given an adaptation number of 1 and similarly *Acer saccharum* 10 representing the two ends of the continuum. The remaining species receive adaptation numbers of intermediate value so that species which frequently occur together and have similar environmental requirements, have the same or closely similar adaptation numbers. Finally the importance value of each species in each sample is multiplied by the adaptation number, the total sum of these values for each stand being termed the *continuum index* of the stand. This index is regarded as a measure of the total environment of a stand of trees expressed in terms of species composition and their relative abundance. Brown and Curtis (1952) give a detailed table of data (Table 8.6) representative of the information extracted by the method from a mass of otherwise extremely variable data. The results are best appreciated as a series of graphs. A considerable scatter of points is usually present and the data is 'smoothed' by a standard procedure given by the formula

$$B = \frac{n_1a + 2n_2b + n_3c}{n_1 + 2n_2 + n_3}$$

where B is the smoothed value of average b and n_1 , n_2 and n_3 are the numbers of stands from which the averages a , b and c have been derived. The relationship between importance value and continuum index is a Gaussian type of curve or part of such a curve (Figs. 8.11 and 8.12), and clearly there is no grouping of curves in zones of the continuum index as should be the case if there were discrete and recognizable associations. On the contrary there is always a continuous overlap of several adjacent leading

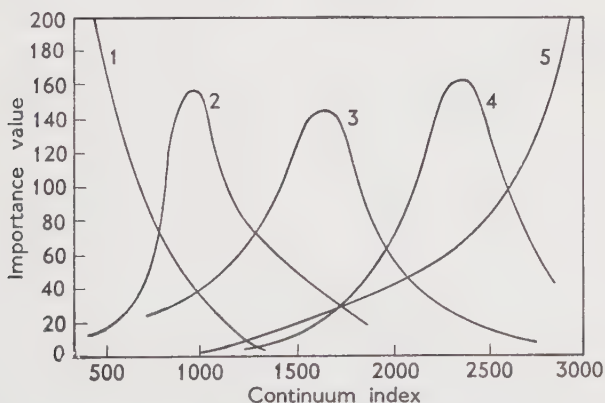


Fig. 8.11. Importance value curves for the five leading tree species (1) *Pinus banksiana*, (2) *P. resinosa*, (3) *P. strobus*, (4) *Tsuga canadensis*, (5) *Acer saccharum*. From Brown and Curtis 1952; courtesy of *Ecol. Monog.*)

Table 8.5—Climax adaptation numbers of tree species found in stands studied.
(From Brown and Curtis 1952; courtesy of *Ecol. Monog.*)

Tree species	Climax adaptation number
<i>Pinus banksiana</i>	1
<i>Quercus ellipsoidalis</i>	2
<i>Quercus macrocarpa</i>	2
* <i>Populus balsamifera</i>	2
<i>Populus tremuloides</i>	2
<i>Populus grandidentata</i>	2
<i>Pinus resinosa</i>	3
<i>Pinus pensylvanica</i>	3
<i>Quercus alba</i>	4
<i>Prunus serotina</i>	4
<i>Prunus virginiana</i>	4
<i>Pinus strobus</i>	5
<i>Betula papyrifera</i>	5
* <i>Juglans cinerea</i>	5
<i>Acer rubrum</i>	6
* <i>Acer spicatum</i>	6
* <i>Fraxinus nigra</i>	6
* <i>Picea glauca</i>	6
<i>Quercus rubra</i>	6
<i>Abies balsamea</i>	7
* <i>Thuja occidentalis</i>	7
* <i>Carpinus caroliniana</i>	7
<i>Tsuga canadensis</i>	8
<i>Betula lutea</i>	8
* <i>Carya cordiformis</i>	8
<i>Fraxinus americana</i>	8
<i>Tilia americana</i>	8
<i>Ulmus americana</i>	8
<i>Ostrya virginiana</i>	9
<i>Fagus grandifolia</i>	10
<i>Acer saccharum</i>	10

* Climax adaptation number of these species is tentative only, because of their low presence in the stands studied.

dominants. Similarly the species with intermediate and with lower importance values show the same overlap over a considerable range of the continuum index. It is of considerable interest that measures of environmental factors taken simultaneously with sampling of each stand show

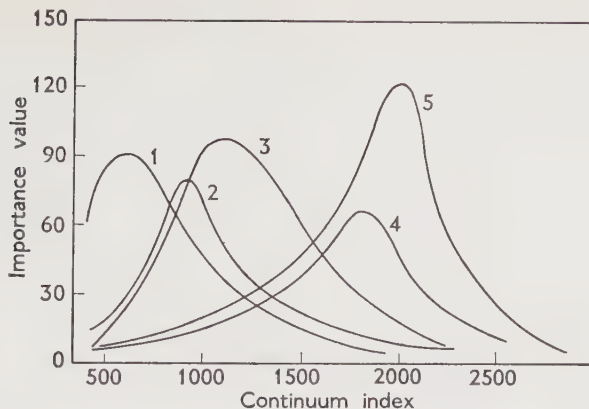


Fig. 8.12. Importance value curves for five intermediate tree species. (1) *Quercus ellipsoidalis*, (2) *Populus tremuloides*, (3) *Quercus alba*, (4) *Betula papyrifera*, (5) *Quercus rubra*. (From Brown and Curtis 1952; courtesy of *Ecol. Monog.*)

marked trends. The specific gravity of screened soil samples, the moisture holding capacity and the available calcium, in the A_1 horizon all follow a very definite trend in relation to the continuum index (Figs. 8.13, 8.14 and 8.15). In addition to the inter-relationship of the species, some interactions between the vegetational continuum and the environment are thus suggested.

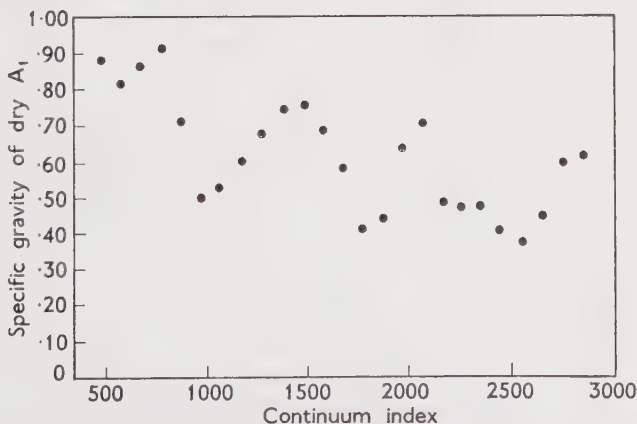


Fig. 8.13. Specific gravity of screened samples of the A_1 soil horizons of stands arranged in 100 unit classes. (From Brown and Curtis 1952; courtesy of *Ecol. Monographs.*)

Table 8.6—Original data for importance values of seventeen species and for three soil characters. (From Brown and Curtis 1952; courtesy of *Ecol. Monog.*)

Stand Number	Continuum Index	<i>Pinus banksiana</i>	<i>Quercus ellipsoidalis</i>	<i>Populus tremuloides</i>	<i>Populus grandidentata</i>	<i>Pinus resinosa</i>	<i>Quercus alba</i>	<i>Pinus strobus</i>	<i>Betula papyrifera</i>	<i>Acer rubrum</i>	<i>Quercus rubra</i>	<i>Abies balsamea</i>	<i>Betula lutea</i>	<i>Tsuga canadensis</i>	<i>Ulmus americana</i>	<i>Tilia americana</i>	<i>Ostrya virginiana</i>	<i>Acer saccharum</i>	Calcium in A ₁ layer (100's lb. per acre)	pH of A ₁ layer	WRC of A ₁ layer
084	356	272	4	9	6	12				4									4.3	5.1	77
066	375	237	46	7			5												4.3	4.9	36
068	467	164	117	4			16												2.9	4.6	54
098	560	157	95	14				5	15	14									2.1	4.6	164
055	594	178		30	7	46		39											1.4	4.5	102
049	664	122	100				62	6		11									2.9	4.0	118
082	721	181		4		34		59	4	4		4							1.1	4.6	99
067	749	100	62	9	8	7	101				5								2.9	4.7	54
113	848	10		68		204		14	3										6.4	4.3	148
064	868		194		24	7		34	16	14	4								—	—	—
039	934		132		27		107		4	3	22								2.1	4.7	60
115	954				4	268		16	12										7.2	5.4	110
150	984		6	54	162	5			30	35	3								—	—	—
053	991			63		159		74	4										—	4.3	400
140	1082			62		116		121											3.6	5.1	281
044	1107		8	4	20	153	11	82	3		18								—	—	—
141	1168	7	4	31	33	65		145		3	7			3					3.6	5.2	400
132	1209				5	138		157											0.7	4.5	269
059	1290		5	4		96		186	7			3							—	—	—
070	1363		32	16			109	46		84									4.3	5.7	43

050	1403	3	3	41	243	10	4	3	3	16	3	3	7.1	4.9	4.9
089	1436			41	238	5	10						0.7	5.2	126
107	1508	15		38	180	3	15	3	40	3			6.4	5.2	106
106	1518	12	18	51	42	21	54	3	84	3			8.6	5.5	180
090	1573		12	15	166	39		13	3	3		3	3.2	5.5	65
105	1582	17		9	158	3	9	82			3	6	8.6	5.0	225
043	1640		5	39	121	7	65	22			20	3	5.4	4.9	89
147	1750	7	22		4	52	20	143	10	7	3		5.4	5.2	272
153	1807	10	10	3	56	96	6	47	16				2.1	5.3	288
086	1888			61	54	12	4			158			0.4	4.0	192
102	1950	4		10	13	20	26	141	3		19		2.7	4.9	91
095	1966		4		106		58		19	84			1.1	5.3	67
101	2060		12	11		3	9	124			3	17	12.5	5.5	80
119	2173	17				11	41	29	7	49	3		35.7	6.1	373
139	2215							6	12	176	4		3.2	4.6	270
138	2234				12		11	3	81				2.1	3.7	409
104	2287	10		11	8	19	15	59	15		17	20	16.0	4.5	289
116	2314	7	28		29	24		33	8				7.2	5.2	209
111	2366				11	32	5		52	157	4		8.6	5.0	223
063	2379				13	6			60	206			-	-	-
136	2404					12		25	72	145			5.4	4.6	400
085	2430				15	12			15	198			14.3	5.5	258
062	2464								66	182	16		7.1	5.6	210
134	2502					28		7	84	87	8		4.3	4.4	335
118	2520							7	29	160	19		12.9	5.0	497
125	2553								58	106	25	34	3.6	5.4	398
034	2591				10	35	5	8	3	27	13	23	45.7	5.6	365
121	2617						4		35	69	49	8	28.6	5.4	131
103	2636								8		80	30	42.8	5.5	305
135	2711							4	22	86	3	18	42.9	6.9	119
080	2747								40	34	11	22	6.4	4.8	158
094	2780								17	13	8	44	23.6	5.3	129
076	2817								3	3	23	8	51.0	7.6	137
133	2852								12		32	16	10.7	5.7	526
114	2938							3	6			8	10.0	5.0	157

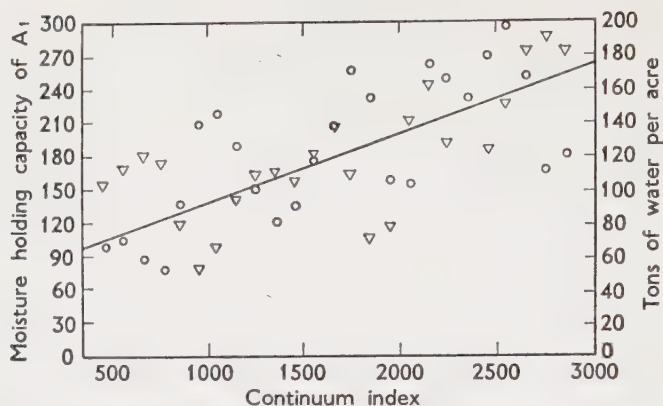


Fig. 8.14. Moisture holding capacity of the A_1 horizon in percentage, and total water held in the entire A_1 horizon at field capacity in tons per acre. Points are average values in 100 unit classes. (From Brown and Curtis 1952; courtesy of *Ecol. Monographs*.)

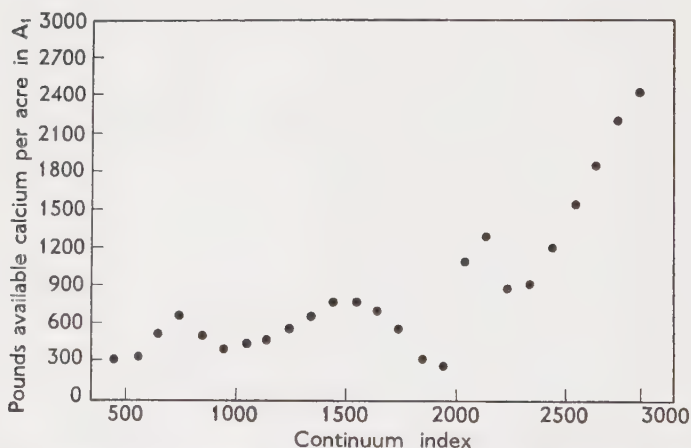


Fig. 8.15. Available calcium in the A_1 horizon in pounds per acre. Points are average values in 100 unit classes. (From Brown and Curtis 1952; courtesy of *Ecol. Monographs*.)

The assignment of the climax adaptation number is necessarily partly subjective and can be criticized on these grounds. However, considerable use is made of the relative importance values of each species within each leading dominant group. Data obtained from limestone grassland in Yorkshire is given below (Tables 8.7, 8.8 and 8.9) to illustrate the point. The data were obtained from a number of sites, frequency and cover repetition (p. 16) being recorded for each species and used jointly as a

Table 8.7—Importance values of the four most abundant species in relation to the leading dominants in an area of grassland in Yorkshire

		<i>Nardus</i>	<i>Agrostis</i>	<i>Festuca</i>	<i>Sesleria</i>
	<i>Nardus</i>	58.6	44.0	49.5	0
Leading dominant	<i>Agrostis</i>	36.0	58.1	50.2	4.5
	<i>Festuca</i>	15.5	37.5	53.9	12.7
	<i>Sesleria</i>	0	13.6	45.1	61.6

measure of the importance value. The limestone area is very variable, the soils ranging from pockets of acidic boulder clay to dark soils immediately overlying limestone rock with a pH above 7.0. The grass cover reflects this wide range of pH, varying from *Nardus stricta* dominated areas to almost pure stands of *Sesleria caerulea*. The importance value calculated from the relative frequency and relative cover of each species, shows *Festuca rubra*, *Agrostis tenuis*, *Nardus stricta* and *Sesleria caerulea* to be the leading dominants in the area. The data are accordingly split into these four groups and importance values calculated for each species (Table 8.7).

The leading dominants ecologically form a series with *Nardus* and *Sesleria* at the two extremes and *Agrostia*/*Festuca* falling in an intermediate position. The importance values in each group confirm this relationship *Agrostis* and *Festuca* having a similar relationship at the acidic end of the scale, but *Festuca* being clearly more closely related to *Sesleria* at the basic end. The remaining species are included in the comparison and importance values calculated for each species in each group (Table 8.8). From

Table 8.8—The importance values of each species present in an area of grassland overlying limestone in Yorkshire in relation to four leading dominants

Species	<i>Festuca</i> group	<i>Agrostis</i> group	<i>Sesleria</i> group	<i>Nardus</i> group
<i>Festuca rubra</i>	53.9	50.2	45.1	49.5
<i>Agrostis tenuis</i>	37.5	58.1	13.6	44.0
<i>Sesleria caerulea</i>	12.7	4.5	61.6	0
<i>Nardus stricta</i>	15.5	36.0	0	58.6
<i>Koeleria gracilis</i>	9.3	0	9.7	0
<i>Thymus drucei</i>	3.8	3.6	11.7	0
<i>Linum catharticum</i>	2.5	0	11.2	0
<i>Viola riviniana/lutea</i>	5.8	3.6	11.4	0
<i>Carex flacca/panicæa</i>	11.9	7.9	18.7	0
<i>Deschampsia caespitosa</i>	3.9	7.9	0	0
<i>Trifolium repens</i>	6.2	0	5.5	0
<i>Potentilla erecta</i>	8.4	0	0	0
<i>Anthoxanthum odoratum</i>	5.1	0	1.0	0
<i>Galium hercynicum</i>	10.6	22.8	0	22.0

Table 8.8 it is now possible to arrange all the species in their relative order and assign to each of them an adaptation number. *Nardus* is arbitrarily designated 1 and is most closely related to *Agrostis*, *Galium hercynicum* is similarly closely related to both *Agrostis* and *Nardus* and in Table 8.8 shows a slightly closer relation to *Agrostis* than to *Nardus*. Accordingly *Galium* is allocated an adaptation number of 3 and *Agrostis* 4 (Table 8.9). The species of maximum importance left in the *Agrostis* group are *Carex* and *Deschampsia* and reference to the *Festuca* group shows *Deschampsia* to be much more closely related to *Agrostis* and accordingly is allocated 5 as its adaptation number. At the other end of the series *Sesleria* is arbitrarily designated as 10, and clearly *Carex* is closely related to it and allocated an adaptation number of 9. Similarly *Thymus*, *Linum*, *Viola* and *Koeleria* are more or less equally related to *Sesleria* and are thus all given an adaptation number of 8. *Festuca* is allocated an adaptation value of 7 and the remaining three species referred to a value of 6. These three species, *Anthoxanthum*, *Trifolium* and *Potentilla*, all have low importance values and are unfortunately of relatively infrequent occurrence in the samples available. It is possible that a larger sample might indicate a reversal of the order of *Festuca* and these three species, but it is unlikely that the present arrangement will unduly influence the continuum indices of the samples. This final arrangement of species is given in Table 8.9.

Table 8.9

Species	Adaptation number
<i>Nardus stricta</i>	1
<i>Galium hercynicum</i>	3
<i>Agrostis tenuis</i>	4
<i>Deschampsia caespitosa</i>	5
<i>Anthoxanthum odoratum</i>	6
<i>Trifolium repens</i>	6
<i>Potentilla erecta</i>	7
<i>Festuca rubra</i>	7
<i>Koeleria gracilis</i>	8
<i>Viola riviniana/lutea</i>	8
<i>Linum catharticum</i>	8
<i>Thymus drucei</i>	8
<i>Carex flacca/panicca</i>	9
<i>Sesleria caerulea</i>	10

Thus the allocation of an adaptation number is based largely on the relative orders of the importance values of each of the species and the element of subjective assessment necessary is slight and restricted to the species with a low percentage occurrence. This can be circumvented by taking a more adequate sample but the labour of such an increase in sample size could be excessive in some instances. The general relationship

of the four most abundant species again shows a considerable overlap of their range (Fig. 8.16) relative to the continuum index and is broadly similar to the results given by Brown and Curtis (1952). There is no

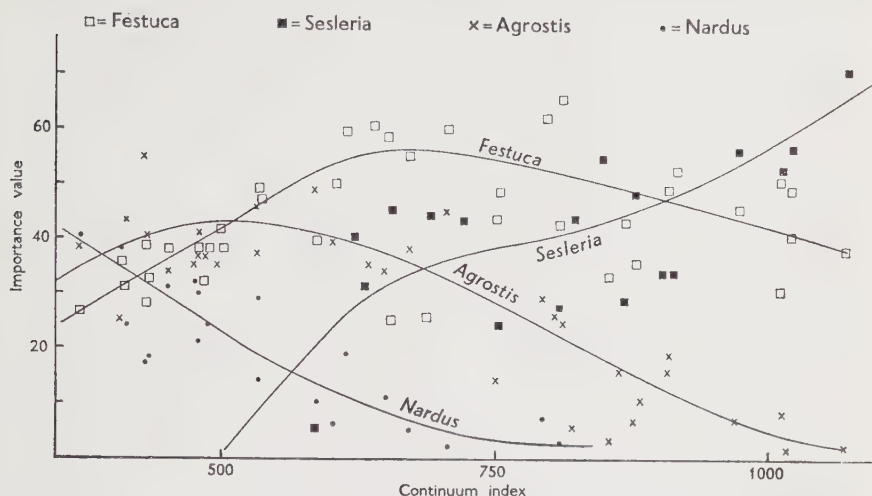
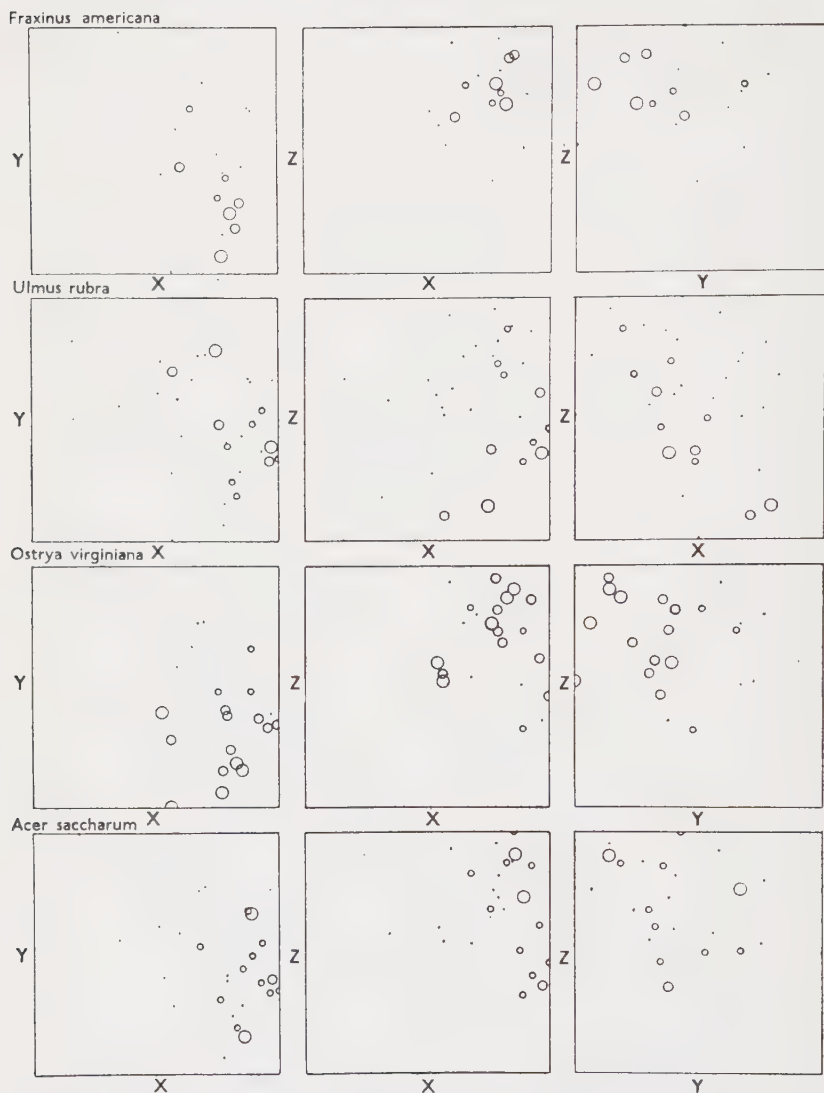


Fig. 8.16. The importance value/continuum index curves for the four leading dominants of sample plots in limestone grassland.

discrete zone solely dominated by one species, or a group of species, but instead there is a continuous variation of composition along the continuum index.

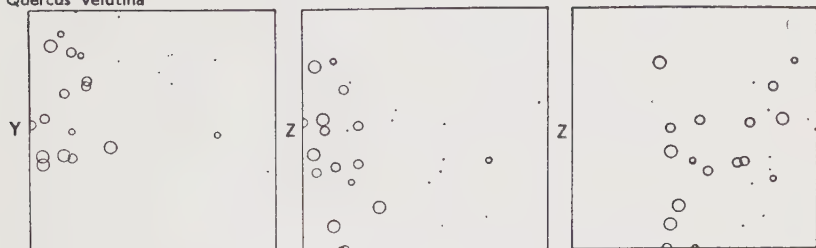
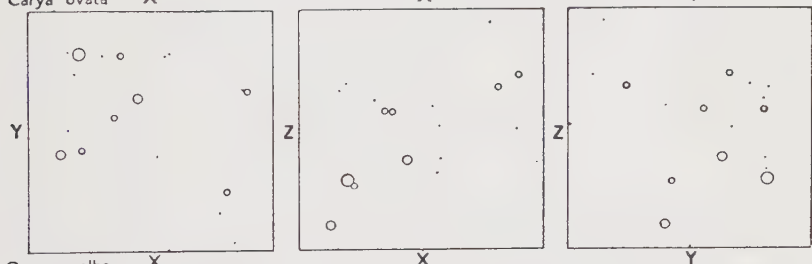
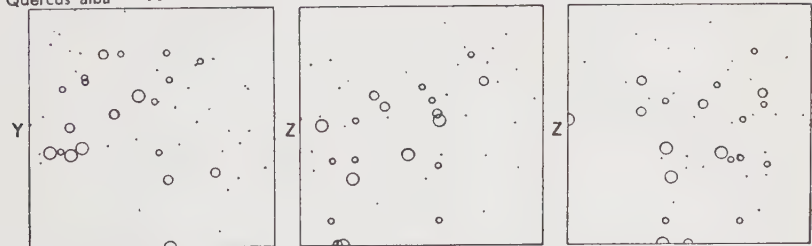
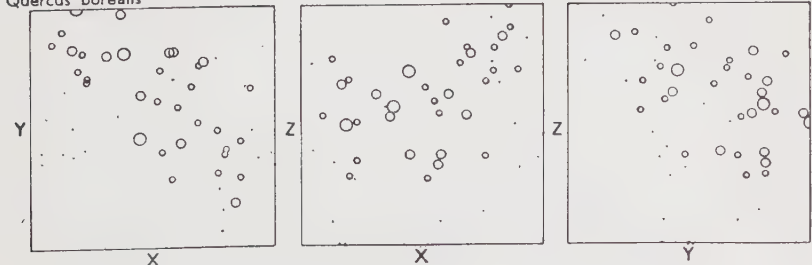
The study of the relationship between the continuum and environment has been extended by the use of a series of coefficients of similarity by Bray and Curtis (1957). The sampling sites were chosen at random as before and quantitative measurements taken of the tree, shrub and herb population in each stand (density and basal area for the trees, frequency for the herbs and shrubs). Fifty-nine stands were sampled and each of these stands was compared with the other 58 and a coefficient of similarity calculated. The coefficient used was that proposed by Gleason (1920), $C = 2w/(a+b)$, where a and b are the quantities of all the plants found in the two stands to be compared and w is the sum of the lesser value for those species common to the two stands. Thus if the two stands were absolutely identical a and b and w would be equal and C then equals 1. Conversely with complete dis-similarity $C = 0$. From the 1,711 values thus obtained the two most dis-similar stands are chosen as the end points of an axis and the remainder of the stands located on the axis by using the inverse value of the other coefficients as ordinates. From this arrangement several stands were found to be more or less equidistant from the two ends of the first

axis but were still very dis-similar. These were examined and the most dis-similar pair again used to establish a second axis. The stands were re-positioned by the two axes, again using the inverse coefficients as co-ordinates. A third axis was finally established on the most dis-similar pair of stands which occurred equidistant from the ends of the axes but which



Figs. 8.17 and 8.18. (opposite) The dominance behaviour of the eight most important tree species at three levels of the ordination. (From Bray and Curtis 1957; courtesy of *Ecol. Monographs*.)

were still very different in composition. From the resultant three axes, each stand is thus located by three co-ordinates to form a three-dimensional spacing. This final positioning in three dimensions produced a highly significant correlation between the spacing of the stands and the original coefficient calculated from the data. From the spatial arrangement of the stands the arrangement of the species can be readily determined although there is some difficulty in representing the three-dimensional spacing on paper. Bray and Curtis give data of the dominant tree species

Quercus velutina*Carya ovata**Quercus alba**Quercus borealis*

(Figs. 8.17 and 8.18). Each species shows a definite spatial 'centre of importance' (related to the number and size of the balls). Away from the centre the concentration and importance of a species diminishes, but not equally in different directions. The three axes are interpreted as: 1. Reflecting recovery from major past disturbance and shows a marked correlation with features of an increasingly mesic environment and with several soil factors—organic matter, pH, Ca, P, etc. 2. Related to drainage and soil aeration and shows correlation with soil water retaining capacity and ammonium ion concentration. 3. Related to recent disturbance and the influence of gap phase replacement.

This clearly confirms the general ecological concept that a large number of inter-related factors control the distribution of a species.

In a linear arrangement of stands as in the original continuum approach described above, the relationship of the stands follows a bell-shaped curve. Similarly in a two-dimensional representation the relationship is contoured and finally of sphaeroid form in three dimensions. Each represents an approximation of the next higher order relationship and the ultimate and exact relationship of a number of stands would be of '*n*-dimensional form'. Such an interpretation concedes the inherent variation of vegetation and equally the continuous variation of the environment, and it necessitates the treatment of data by a statistical technique of factor analysis. Such an approach is possible and indeed has been made (see Goodall 1954*b*) but is rather beyond the scope of this present discussion (see below). Furthermore, the time consuming nature of both the sampling and computation involved has to be carefully considered in relation to the value of the information gained. It seems reasonable to accept a good approximation in one, two or three dimensions, with a minimum amount of computation, though the recent developments in the world of electronic computers may well make the use of high-powered techniques worthwhile in the future. However, the ordination methods developed by Curtis and his associates have underlined the extreme difficulty of defining 'communities' and 'associations'. This is summarized by Bray and Curtis: 'Each species has a separate area of location, and within this area its distribution is interspersed to varying degrees with other species distributions so that there is a continuous change in stand composition from any part of the ordination to any other part.'

DISCUSSION

In general, the methods of approach to the problem of classifying vegetational units fall between two schools that have developed, apparently representing two extremes. Braun-Blanquet erects a series of units, or associations, which can be classified in an hierarchical system,

and are distinct, recognizable and definable entities. Curtis and his associates on the other hand regard vegetation as a multi-dimensional continuum, no two stands being the same. These two schools of thought are a direct result of the sampling methods employed, non-random on the one hand and random (or approximately so) on the other. Thus the careful choice of stand with the stipulations of minimal area and homogeneity is highly subjective, and initially at least, only the central 'nodum' (see Poore 1955-6) being isolated, characterized and described. The numerous intermediates are ignored. At a later stage the more obvious intermediates can possibly also be considered, and described as 'associations' or 'facies'. It is debatable whether this ultimate stage is possible in practice. Such an ultimate stage in fact, represents a continuum in the sense of Curtis *et al.* where a random selection of sites necessarily includes 'noda' and intermediates alike. The continuum approach does not produce anything which can be classified, the ordination shows instead the inter-relationships between the species which are believed to be controlled by environmental gradients. However, having obtained this detailed information from an area of grassland for example, one still talks of a *Sesleria* association, or an *Agrostis*/*Festuca* association or a *Nardus* association purely for convenience. The presence of a large number of intermediates is certainly accepted but the noda are very useful concepts. Implicit here seems to be the *frequency of occurrence* of a particular range of stand variation; a *Sesleria* association is variable but in an area of limestone grassland it is a very common unit, much more so than the intermediate *Festuca*/*Sesleria* stands. The two extreme schools of thought based on random or subjective choice of samples in fact offer two useful ecological approaches. Man always seems to want to classify and an orderly arrangement of vegetational units is certainly a desirable and useful objective. Conversely it is equally desirable to study in detail gradients of an environment and their effect on species composition. Both are equally valuable.

It is informative to consider at this point which features of a stand of vegetation make a visual impact on the observer. It is not merely the presence of a number of species which form the basis for description but their density, distribution, size, growth-form and their vigour. Thus ideally any classificatory system should be based on the species present, and also on measures of their abundance, distribution, size and vigour. The samples should be taken randomly, relative to the vegetational 'type' to be studied, i.e. 'woodland', 'grassland', etc. and the ordination or classification should be based on an objective method. On this basis the Braun-Blanquet approach falls short of the ideal. It is based on non-random sampling, it employs the measure of presence or absence only to characterize the association, and although some estimate of abundance is available from the description of the stands in the field, little or no subsequent use appears to

be made of it. Finally, the ultimate sorting of the data is not objective. Its success lies in its relative simplicity and in a modified form, in the erection of 'defined' noda. Since it is useful to have conveniently labelled 'noda' the method is of considerable value in describing areas which have not previously received any ecological attention. The use of χ^2 contingency table and the subsequent arrangement of a system of units either hierarchical or spatial, similarly falls short of the ideal. The method employed by Williams and Lambert picks out species groupings which are given artificial boundaries since at each stage of the procedure the quadrats are repeatedly divided into those with and those without a certain species. This is highly artificial but it produces a map of the area studied, with arbitrary lines drawn on the boundaries of the spatial limits of a species or groups of species. Subsequently detailed attention can be directed to those parts of the 'map' which are markedly different and these differences investigated in relation to the local environmental factors.

The Curtis school have made an approach which is the nearest to the theoretical ideal proposed above and it yields information of considerable value. Clearly though, it would be impractical to attempt such a project in the centre of the Amazon Basin where no ecological work has been previously attempted. In this instance a simpler approach would be necessary and the Braun-Blanquet system would under these conditions be the most useful. Thus the primary need is the establishment of recognizable associations. Once these are established a more detailed approach can be usefully made, and the ordination in several dimensions of Bray and Curtis seems to offer a very convenient technique of this type. Again this approach is an approximation to the theoretical situation of n -dimensional species space, where the more elegant techniques of discriminant or factor analysis are valid. Thus Harberd (1962) used discriminant analysis to study the relationship of a number of *Agrostis*/*Festuca* stands and it would seem this type of analysis may be of considerable value.

With this more elaborate statistical procedure it is necessary to have a quantitative measure of the abundance of the species in each plot. The analysis of the data is made more worthwhile, and the value of the results is considerably increased if in each plot several measures of abundance are used (e.g. density, cover, frequency and performance) together with quantitative measures of the more important environmental factors. The labour involved in assessing, on this scale, a large number of stands would obviously have to be seriously weighed against the relative value of the information obtained. Thus a number of methods are available, each with its own limitations but each of considerable value within certain limits. The final choice of method is therefore dependent both on the amount of detailed information required and on the amount of time available and the simpler methods on these considerations have much to recommend them.

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